VOL. XV APRIL 1961 NO. 2

PACIFIC SCIENCE

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Studies on Spawning Behavior, Egg Masses, and Larval Development in the Gastropod Genus *Conus*, Part I Observations on Nine Species in Hawaii[1]

ALAN J. KOHN[2]

THIS REPORT deals chiefly with the characteristics of egg masses and the course of larval development of gastropod mollusks of the genus *Conus*, based on material collected in the Hawaiian Islands during 1954–56, while the author was at the Hawaii Marine Laboratory. Some information has been obtained on 9 of the 33 species of *Conus* known to occur in the Hawaiian archipelago (Kohn, 1959*a*).

Bergh stated (1895: 100), "Ueber Paarung, Eilegen und Laich der Coniden ist ... absolut nichts bekannt."

The only reference prior to that date which has come to the attention of the present writer is an extremely brief description of the oöthecae or egg capsules of *C. capitaneus* Linnaeus by Adams and Adams (1853: 5). Cooke (1895) and Hornell (1922) figured egg capsules of unidentified species of *Conus*, but Lamy (1928), in an extensive study of prosobranch egg capsules, noted their similarity to those of other genera. These early figures cannot be assigned with certainty to *Conus*, and Bergh's statement remained essentially correct until Petit and Risbec (1929) and Risbec (1931, 1932) described the egg masses and development of four species of *Conus* from New Caledonia. Subsequently, similar information on six additional species has been reported by Thorson (1940), Persian Gulf; Lebour (1945), Bermuda; Knudsen (1950), West Africa; Natarajan (1957), India. More recently Lewis (1960) has provided additional information on the egg capsules and larvae of *C. mus* Hwass *in* Bruguière, a species discussed also by Lebour (1945).

Ostergaard (1950) described the spawning and development of six species of *Conus* in Hawaii. The present paper provides information on five additional species and notes on development in one species mentioned by Ostergaard but not studied in detail by him.

Most of the material was collected on coral reefs which fringe much of the Hawaiian coastline and provide suitable spawning sites for a number of species of *Conus* (Kohn, 1959*b*). Bouin's solution and 10 per cent sea water formalin were used as fixatives. Except where stated otherwise, all material was collected by the author, and the numbers used to identify specimens are those of the author. The preserved egg capsules and embryological material have been deposited in the University Zoological Museum, Copenhagen.

GENERAL CHARACTERISTICS OF SPAWNING AND EGG MASSES

As is typical of the higher prosobranch gastropods, the sexes are separate and fertilization is internal. The prominent penis of the male is a flattened muscular tube which arises from the right side of the dorsolateral body wall just behind the head and is rounded or pointed at the tip (Bergh, 1895: 97, figs. 4, 5, 76, 149, 159).

In copulation, it is inserted into the vagina of the female, which is located anteriorly at the extreme right edge of the mantle cavity, where the mantle joins the body wall, and adjacent to the anus (unpublished observations). A detailed account of the genital apparatus of prosobranchs has been given by Fretter (1941, 1946).

Although the process of oviposition in *Conus* has not been studied closely, it is essentially similar to that first described in other higher prosobranchs (Order Neogastropoda) by Cunningham (1899) and later amplified by Ankel (1929), MacGinitie (1931), and Ino (1950). Eggs surrounded by albuminous, probably nu-

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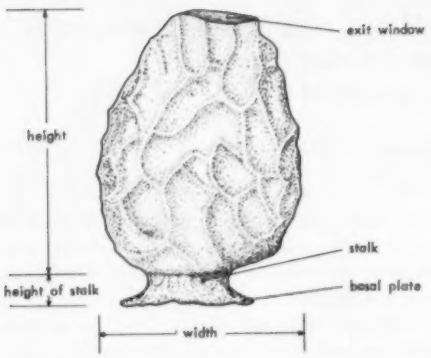


FIG. 1. Generalized egg capsule of *Conus*, with terms used in presentation of dimensions.

tritive, material are passed out of the genital aperture of the female downward through a temporary groove on the side of the foot to the egg capsule gland, which is situated on the anterior portion of the sole. The fluid mass of eggs passes into the aperture of the gland, in which horny egg capsules are produced. This method of egg capsule formation is characteristic of the Neogastropoda, in contrast to the Mesogastropoda in which the capsule is secreted in the genital ducts and only moulded and hardened by the egg capsule gland (Ankel, 1929; Fretter, 1941).

The general shape of the capsules (see Fig. 1) is "like a flattened pouch or flask" (Knudsen, 1950). As will be shown below and in a forthcoming paper (Kohn, MS), there is a moderate degree of interspecific variation in the form of the egg capsules and, in some species, considerable intraspecific variation. It is usually not possible to determine the species to which an egg mass belongs in the absence of the parent. This is in marked contrast to the egg capsules of some other prosobranch genera, e.g., *Murex* and *Nassa*, which are highly species-specific (Thorson, 1959).

The capsule is typically white or straw-colored and is presumably constructed of conchyolin, a scleroprotein. The capsules are deposited in clusters which frequently consist of several short rows of a few capsules each. A cluster of egg capsules is referred to as an egg mass, following Thorson (1940, *et seq.*) and others. The number of capsules deposited in a cluster and the number of eggs per capsule are variable. In the material collected in Hawaii, the number of capsules per cluster ranged from 1 to 68 (Table 1) and the number of eggs per capsule from 80 to about 10,000 (Table 2).

In most species, each capsule is attached to the substratum, usually the underside of a rock, by an adhesive basal plate (Fig. 1). There is a narrow, short stalk, above which is the capsule proper. Its walls are thin, nonrigid, and translucent, and they usually bear ridges on the flat surfaces. The lateral edges are typically convex, and there is a preformed exit window along the straight, uppermost part of the capsule. It is covered by a hyaline membrane or operculum, which is never very thick and appears to become thinner and more transparent as development proceeds. The hatching process has not been studied closely, but it appears that the entire membrane dissolves prior to escape of the larvae. This is in contrast to the family Muricidae, in which the egg capsule is closed by a thick operculum which is lost intact at hatching (Ankel, 1937; Hancock, 1956). Dissolution of the operculum may be due to an enzyme liberated by the larvae just prior to hatching (Ankel, 1937). The larvae of *Conus* do not occupy the entire capsule before hatching.

DEVELOPMENT WITHIN EGG CAPSULE

To study the course of larval development, egg masses were kept in constantly aerated running sea water in finger bowls or wide-mouth 4-l. jars. Following hatching, the larvae were kept in the larger jars in aerated, but not circulating, sea water. In some cases, sand and coral rocks from the normal habitat were placed on the bottom of the vessel in an effort to induce settling of the larvae, but this was generally unsuccessful. Details of embryonic development are described below for those species in which they could be determined, and present knowledge of development in *Conus* is reviewed in the section, Discussion.

Conus abbreviatus Reeve

A cluster of 33 egg capsules was found attached to the underside of a metal refuse can

TABLE 1

COLLECTION RECORDS AND CHARACTERISTICS OF EGG MASSES OF *Conus* IN HAWAII

SPECIES	LOCALITY[1]	DATE OF COLLECTION	SPECIMEN NUMBER	NO. OF CAPSULES IN CLUSTER	HEIGHT × MAXIMUM BREADTH OF CAPSULES (mm.)
abbreviatus	Waikiki	15 III 1923	(Ostergaard, 1950)	12	10 × 8
abbreviatus	Diamond Head	10 III 1956	1382	33	9 × 7–7.5
catus	Waikiki	12 VI 1922	(Ostergaard, 1950)	19	12 × 9
catus	Paia, Maui	5 VIII 1956	2180	1	12 × 10
catus	Koko Head	22 VIII 1956	2299	3[2]	11–12 × 10
catus	Koko Head	22 VIII 1956	——	4	10–11 × 8.5–9.5
ebraeus	Waikiki	22 III 1921	(Ostergaard, 1950)	—	10 × 10
imperialis	Diamond Head	6 VII 1956	1983	6[2]	18–20 × 12–13
leopardus	Kaneohe Bay	25 IV 1956	——	19	49–58 × 34–37
lividus (?)	Maile	7 II 1956	1264	36, 30	10.5–12 × 10–12; 9–10 × 8.5–10
pennaceus[4]	Waikiki	19 V 1921	(Ostergaard, 1950)	34	11 × 8
pennaceus[4]	Waikiki	25 V 1922	(Ostergaard, 1950)	—	——
pennaceus	Waikiki	26 VII 1954	156	20	8.5 × 7.5
pennaceus	Waikiki	4 VIII 1955	——	38	——
pennaceus	Diamond Head	13 VIII 1955	401–404	68, 50, 25, 9	——
pennaceus	Hauula	9 VI 1956	1811	34	9–10.5 × 7–8
pennaceus	Mahie Point	9 VI 1956	1810	58	9.5–11 × 7.5–9
pennaceus	Diamond Head	10 VI 1956	——	68	12–13 × 9–10
pennaceus	Diamond Head	4 VII 1956	1962	10	9–11 × 8
quercinus	Kaneohe Bay	9 II 1956	——	40	19–26 × 17–22
quercinus	Kaneohe Bay	9 II 1956	——	3	17–19 × 18–20
rattus	Waikiki	4 VIII 1921	(Ostergaard, 1950)	22	15 × 11
rattus (?)	Waikiki	21 III 1956	——	31	12–14 × 11–14
vexillum[5]	Waikiki	16 V 1921	(Ostergaard, 1950)	34	20 × 13
vitulinus	Ala Moana	7 VII 1956	2020	11	23 × 16–17
vitulinus	Diamond Head	VII 1957	——	—	——

[1] All from the island of Oahu unless otherwise indicated.
[2] Oviposition possibly interrupted by collector.
[3] Oviposition definitely interrupted by collector.
[4] This species is referred to as *C. omaria* Hwass by Ostergaard (1950).
[5] This species is referred to as *C. sumatrensis* Hwass by Ostergaard (1950).

cover in 1 m. of water on the reef at Diamond Head, Oahu, 10 March 1956. The capsules (Fig. 2) were affixed to their substratum in three rows of 12, 17, and 14. Two adult *C. abbreviatus* (no. 1382, ♀, 29 × 21 mm.; no. 1383, sex undet., 32 × 21 mm.) were found about 1 m. from the can lid, which appeared to be the nearest available protected site for oviposition, since all nearby coral rocks were buried to a depth below the oxidized surface layer of sand. This egg mass is tentatively assigned to *C. abbreviatus* because of the proximity of the adults and the close similarity with the egg capsules of that species described by Ostergaard (1950).

The shape of the capsules is typical of the genus. They are slightly higher than broad and are affixed to the substratum by a short stalk and broad basal plate. The capsular walls are smooth except for peripheral ridges on one side (Fig. 2*b*) and two ridges extending downward from near the upper corners on the opposite side (Fig. 2*c*). Both lateral edges of the capsule are convex. The characteristics of the egg mass are summarized and compared with that studied by Ostergaard (1950) in Tables 1 and 2.

In order to study the course of development, the egg mass was placed in aerated circulating sea water. One egg capsule was removed from the cluster and its contents examined on the day of collection. The embryos, which were pink in color when viewed through the translucent capsular wall, were found to be in the blastula

stage, with the four macromeres and many micromeres distinctly visible. It is likely that the embryos were 1–2 days old. They were oval in shape, measured 175–200 × 165–175 μ, and were slowly motile when released from the capsule into sea water. The blastula is the earliest stage at which activity is observed in *Conus* embryos (Ostergaard, 1950).

An egg capsule opened on the second day after collection contained motile embryos which resembled early trochophores (Fig. 3*a*). The resemblance of this stage to typical trochophore larvae is somewhat closer in *C. abbreviatus* than in other species of *Conus* (see below and Ostergaard, 1950) in which the trochophore stage is suppressed. This is typical of gastropods in which this stage is passed within an egg capsule or brood pouch (Raven, 1958).

The trochophore-like embryos of *C. abbreviatus* measured 270 × 170 μ and retained the pink color of the previous stage. On the fourth day after collection, the first traces of shell were visible (Fig. 3*b*). Two days later, velar lobes were beginning to form (Fig. 3*c*) and the embryos, which now measured 255 × 150–165 μ, swam actively when released from the capsule. On the 9th day after collection the velar lobes and larval shell appeared to be fully developed (Fig. 3*d–f*). The pink color persisted, and the shells were transparent and bore numerous fine nodules (Fig. 3*d, e*). Otocysts, eyes, heart, foot, and operculum were easily visible. The maximum dimension of the shell was 270 μ, and the breadth of the velar lobes was about 250 μ. The veligers were motile within the capsule and swam actively when released from it into sea water. No further development was detected on the 11th day after collection. On the 13th day after collection, presumably the 14th or 15th day after oviposition, some veligers hatched from egg capsules following apparent dissolution of the exit window. The hatched veliger larvae closely resembled those in Figure 3 *d–f* but measured 275–300 μ in maximum shell dimension. They swam freely in the container and were colorless except for a row of green pigment spots inside the margins of the velar lobes (Fig. 3*e, f*). Unhatched veligers within the capsule retained the pink color in the visceral mass.

FIG. 2*a*. Egg capsules of *Conus abbreviatus* Reeve. Diamond Head, Oahu, 10 March 1956. Portion of a row of capsules affixed to metal can lid.

Within two days the rest of the veligers appeared to have hatched from the capsules. During the ensuing 10 days no further development was observed and none of the larvae settled to the bottom of the container to assume the benthic mode of life. By the 11th day after hatching, all of the larvae were dead and the observations were terminated. The course of larval development is summarized and compared with that of other species in Table 3.

Conus catus Hwass *in* Bruguière

A specimen of *C. catus* (no. 2180) collected at Lower Paia, Maui, on 5 August 1956, was observed to have affixed a single egg capsule to its shell about 2 hr. after collection. The capsule measured 12 × 10 mm.

On 22 August 1956, a female *C. catus* (no.

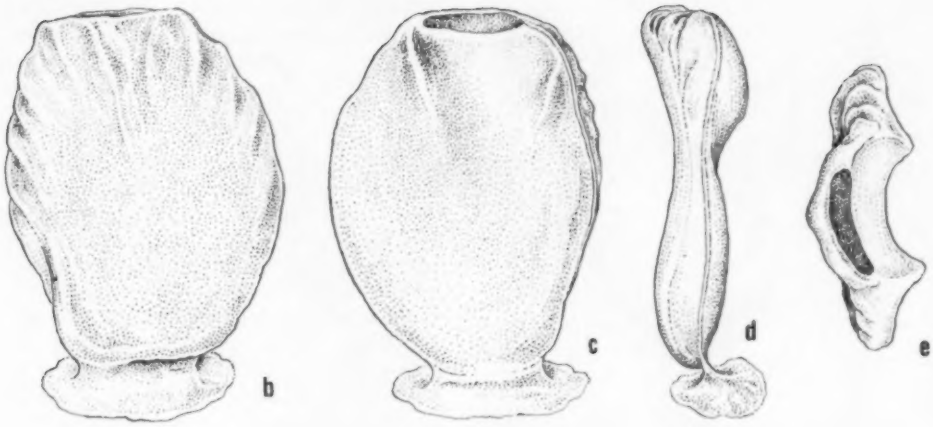


FIG. 2*b–e*. *b,c,d*, Side and edge views of one capsule; *e*, top view of another capsule.

2299, 40 × 26 mm.) was found ovipositing at Koko Head Sandy Beach, Oahu, by M. A. Kohn. Three capsules had been deposited, and spawning probably would have continued had not the adult been disturbed. However, a second cluster of 4 essentially identical capsules, unaccompanied by an adult, was also collected (Table 1). Ostergaard (1950) figured 19 capsules in an egg mass of *C. catus*.

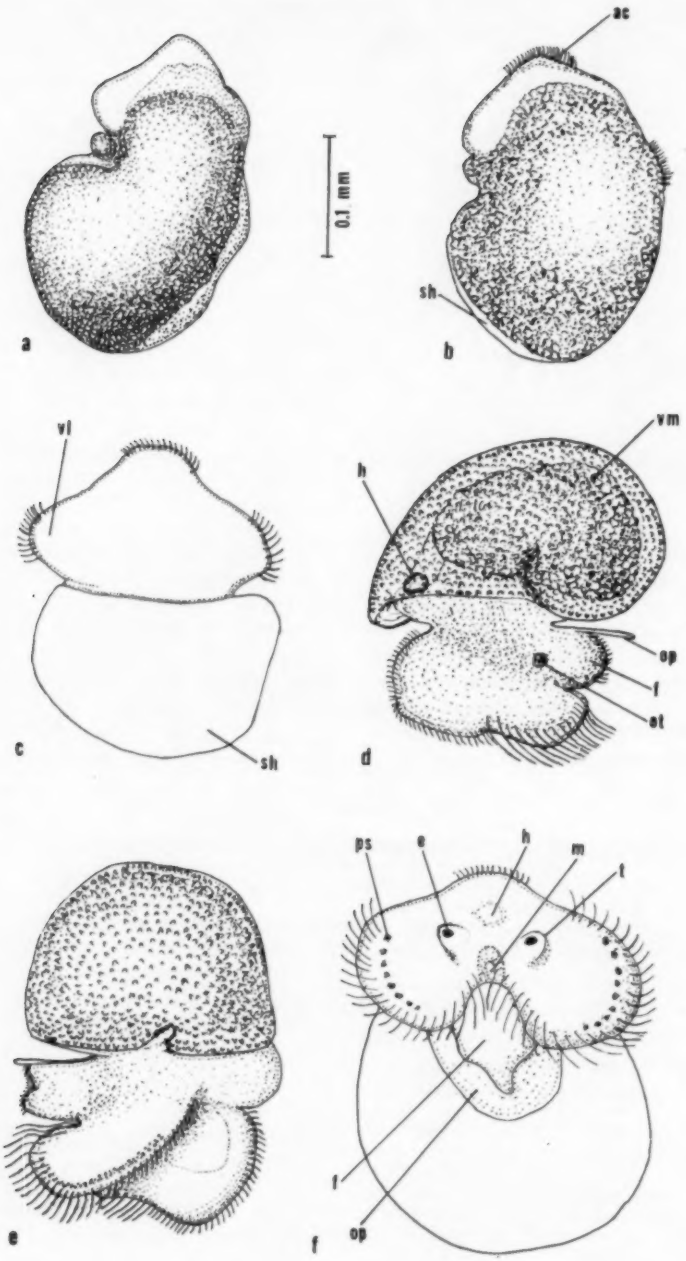
The form of the egg capsules of *Conus catus* is typical, although the stalk is somewhat taller than in other species of the genus (Fig. 4). The lateral edges are slightly convex; the upper edge is quite straight. Capsules in both clusters contained embryos in the 4-cell stage which measured 250–300 μ across. A few uncleaved eggs 235 μ in diameter were present in one capsule. The characteristics of these egg masses are sum-

TABLE 2

NUMBER OF EGGS PRODUCED, EGG DIAMETER, LENGTH OF DEVELOPMENT BEFORE HATCHING, AND STAGE AT HATCHING OF *Conus* IN HAWAII

SPECIES	AVERAGE NO. EGGS/CAPSULE	AVERAGE NO. EGGS/EGG MASS	AVERAGE EGG DIAMETER (μ)	TIME OF DEVELOPMENT IN EGG CAPSULE (days)	STAGE AND SIZE AT HATCHING	
abbreviatus	1,300	44,000	200	14	veliger	270μ
catus	1,650	15,000[1]	220	15–16[1]	veliger	375μ[1]
ebraeus	——	——	——	——	veliger[1]	280μ[1]
imperialis	5,900	(35,400)	225	——	——	——
leopardus	2,950	56,000	——	——	veliger	360μ
lividus (?)	——	——	——	——	veliger	250μ
pennaceus[2]	80	3,500	460	16[1]	veliconcha	1200μ
quercinus	9,700	210,000	215	15–16	veliger	285μ
rattus	2,000[1]	44,000[1]	125[1]	——	(?)veliger	240μ
vexillum[3]	"thousands"[1]	——	140[1]	12[1]	veliger	250μ[1]
vitulinus	——	——	225	14–15	veliger	360μ

[1] Data from Ostergaard (1950).
[2] This species is referred to as *C. omaria* by Ostergaard (1950).
[3] This species is referred to as *C. sumatrensis* by Ostergaard (1950).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marized in Tables 1 and 2. It was not possible to follow the course of larval development, but Ostergaard (1950) has described the development of *C. catus* in some detail.

Conus imperialis Linnaeus

A female *C. imperialis* (no. 1983, 79 × 23 mm.) was observed ovipositing in a depression on the side of a large dead coral head in 0.3 m. of water at Diamond Head, Oahu, on 6 July 1956. Six capsules had been deposited when the rock was turned over and oviposition was interrupted. The capsules are rather long and narrow, measuring about 19 × 13 mm., and do not rise vertically from the stalk and basal plate but are skewed to one side (Fig. 5). Upon return to the laboratory, one of the capsules was pierced and some of its contents withdrawn with a pipette. The eggs were uncleaved and measured 225 μ in diameter. Eggs in the same capsule had not undergone the first cleavage 3.7 hr. later. Twenty-four hr. later, however, eggs in the same capsule had progressed to the 4-cell stage, which measured 250 μ on each side and resembled the 4-cell stage of *C. quercinus* (Fig. 12*c*).

On the 3rd day after oviposition, a second capsule was examined and found to contain embryos in the blastula stage. No further development took place in the cultures and all of the embryos appeared to be dead and were fixed on the 16th day after oviposition. The egg masses and larval development, as far as it could be studied, agree closely in the same species studied in the Seychelles Islands (Kohn, MS). The characteristics of the egg mass from Oahu are summarized in Tables 1 and 2.

Conus leopardus (Röding)

A cluster of 19 very large egg capsules was found adrift in Kaneohe Bay, Oahu, at a depth of 5 m. by A. H. Banner on 25 April 1956. The basal plates of the capsules were confluent, holding the entire mass together. A bright green filamentous alga was associated with the egg mass when it was collected. However, the original substratum from which the mass presumably became detached is not known. The largest capsule measured 58 × 37 mm., exclusive of stalk and basal plate, and the average size was 54 × 35 mm. This is about twice as large as any other known *Conus* egg capsule. For this reason the egg mass is tentatively assigned to *C. leopardus*, which is by far the largest species in the family in Hawaii, reaching a length in excess of 20 cm. The capsules were collected in an area where *C. leopardus* is known to occur.

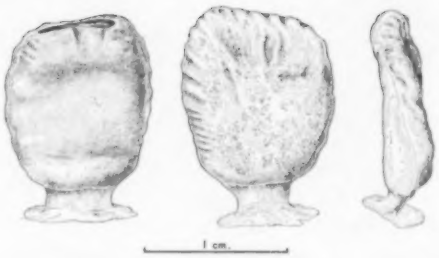

FIG. 4. Views of an egg capsule of *Conus catus* Hwass *in* Bruguière. Koko Head, Oahu, 22 August 1956.

The capsules differ in shape from those of other species of *Conus* by having one lateral edge concave (Fig. 6). The capsular wall is roughened by numerous irregular ridges.

It was not possible to examine the contents of the egg capsules until 2 days after collection. At that time typical veliger larvae, measuring 345 μ in maximum shell dimension, were present. Thus although the adults and egg capsules of *C. leopardus* are very large, the veliger larvae, and presumably the eggs, are not significantly larger than those of much smaller species (Table 2). Indeed the veligers are much smaller than those of *C. pennaceus* (Table 3), the adults of which species are typically one-fourth or less the size of *C. leopardus*.

FIG. 3. Developmental stages of *Conus abbreviatus* Reeve. *a*, 3- or 4-day embryo, in modified trochophore stage; *b*, 5- or 6-day embryo, with first trace of shell present; *c*, 7- or 8-day embryo, showing developing velar lobes; *d*, fully-formed veliger, 10 or 11 days, lateral view; *e*, as *d*, but anterior-lateral view; *f*, as *d*, but anterior-ventral view, showing expanded velar lobes and ventral aspect of foot and operculum. *ac*, Apical cilia; *e*, eye; *f*, foot; *h*, heart; *m*, mouth; *op*, operculum; *ot*, otocyst; *ps*, pigment spot; *sh*, shell; *t*, tentacle; *vl*, velar lobe; *vm*, visceral mass.

TABLE 3

COURSE OF EMBRYONIC DEVELOPMENT IN HAWAIIAN *Conus*

DAYS AFTER SPAWNING[1]	*C. abbreviatus*	*C. pennaceus*	*C. quercinus*	*C. vitulinus*
0–1	blastula (200μ)[2]	early cleavage stages (460μ)	uncleaved eggs (200μ)	early cleavage stages (225μ)
2–3	early trochophore (270μ)		early blastula	blastula (225μ)
4–5	well-developed trochophore (240μ)	late trochophore	blastula (200μ)	
6–7	early veliger (255μ)		trochophore (240μ)	trochophore (360μ)
8–9			early veliger (315μ)	veliger (385μ)
10–11	well-developed veliger (270μ)	well-developed veliger (780μ)	well-developed veliger (275μ)	
12–13			well-developed veliger (285μ)	
14–15	hatching (veliger) (300μ)		hatching (veliger) (290μ)	hatching (veliger) (370μ)
16		hatching[3] (veliconcha) (1200μ)		
17–25	no further development			

[1] Probable in *C. abbreviatus*.
[2] Maximum dimensions are indicated in parentheses.
[3] Data from Ostergaard (1950).

Only 2,950 veligers were present in the one capsule which was counted, and they occupied but a small portion of the capsule. As in several other species, yellowish-green pigment spots about 10 μ in diameter were present inside the margins of the velar lobes. A large operculum, a pair of otocysts, each containing an otolith, and black eyes were present. The long (*ca.* 75 μ) velar cilia beat slowly and metachronally. The larval shell was transparent but covered with minute (*ca.* 2 μ) raised dark nodules. The visceral mass appeared white within the shell.

Several hours later on the same day, hatching began and the hatched veligers, which measured 360 μ in maximum shell dimension, swam about slowly in a 4-l. jar of aerated sea water. On the following day, the jar was densely populated with freely swimming veligers, which swam more rapidly than on the previous day. The population was then divided between two 4-l. jars. Three days later, most of the veligers had died. Four of those which remained alive were placed in a large Stender dish (*ca.* 120 mm. in diameter) containing sea water and sand from the reef. Of these, three continued to swim about, but one settled to the bottom, where it actively beat its cilia and possibly engaged in feeding. If disturbed, it swam actively for a few seconds, then returned to the bottom. However, it was not observed to crawl on its foot, nor was there any evidence of resorption of the velar lobes or other manifestation of metamorphosis. On the following day, all four larvae in the dish were dead. Two days later, the 6th day after hatching, a few swimming veligers remained in one jar, but the observations had to be terminated.

Conus lividus Hwass *in* Bruguière (?)

On 7 February 1956, at Maile, Oahu, two clusters of straw-colored egg capsules were found affixed to the underside of a coral rock, under which a large female *C. lividus* (no. 1264, 45 × 26 mm.) was also present. One cluster consisted of 36 egg capsules, all of which were empty, and the other contained 30 capsules, some of which contained dead veliger larvae. Since these capsules were probably deposited

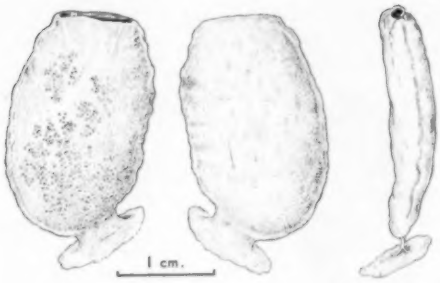

FIG. 5. Views of an egg capsule of *Conus imperialis* Linnaeus. Diamond Head, Oahu, 6 July 1956.

two or more weeks prior to their collection, it is by no means certain that the adult female associated with them was the parent. Indeed, it is not certain that the capsules are actually those of *C. lividus*, and the identification is tentative. It is supported, however, by morphological similarities with capsules known to have been deposited by *C. lividus* in other areas (Kohn, MS).

The capsules are distinguished from those of several other species of *Conus* by being somewhat more discoid in form and bearing crenations along the edges of the otherwise rather smooth capsular wall (Fig. 7). There are also two more or less parallel ridges extending downward from the corners of the exit window, as in *C. abbreviatus*. The capsules in the smaller group, shown in Figure 7, averaged 11 mm. in height and maximum breadth. The capsules in the other group were essentially similar in appearance but were slightly smaller, averaging 9.5 mm. in both dimensions.

The veliger shells, 235–260 μ in maximum dimension, were yellowish brown and bore minute densely-packed, raised, darker brown nodules over the entire surface.

Conus pennaceus Born

Egg masses of *C. pennaceus* have been collected on numerous occasions in Hawaii (Table 1). As noted by Ostergaard (1950) the egg mass of *C. pennaceus*[3] differs from those of other species in that only a few capsules are attached directly to the substratum. Most are affixed to previously deposited capsules, thus forming the "arches and bridges" mentioned by Ostergaard and making the entire mass very compact (Fig. 8). The individual capsules are typical of the genus (Fig. 9).

In the present study, 10 egg masses of *C. pennaceus* were collected on seven occasions, all in the months of June, July, and August (Table 1). The 2 egg masses reported by Ostergaard (1950)[3] were collected in May. The data suggest May–August as the breeding season of this species.

The development of *C. pennaceus* from fertilized egg to hatching has been described and illustrated by Ostergaard (1950). It was possible to follow portions of the course of larval development in 2 of the egg masses listed in Table 1.

On the day after collection, the egg mass from Diamond Head, Oahu, 10 June 1956 (which was found adrift over the reef by P. Helfrich), contained early veliger larvae which appeared to be in the later stages of torsion. A very small shell rudiment, a slowly beating heart, and eyes were present. On the 4th day after collection, the veligers appeared to be between the stages shown by Ostergaard's figures 11d and 11e, or probably about 12–13 days from oviposition. The siphonal canal of the shell had begun to form, and a row of chartreuse pigment spots was present along the margin of the velar lobes.

During the next 7 days, the shells gradually grew to 1.1 × 0.7 mm., and the wall of the exit window became thinner and more transparent, but no capsules hatched. Hatching of a few capsules finally occurred on the 16th day after collection. This probably corresponded to 25–26

FIG. 6. Egg capsules of *Conus leopardus* (Röding). Kaneohe Bay, Oahu, 25 April 1956. *a*, Side view of one capsule; *b* and *c*, opposite side and edge views of another capsule.

[3] This species is referred to as *C. omaria* Hwass by Ostergaard (1950).

days after oviposition, an abnormally long embryonic period compared with other species and with Ostergaard's observations on *C. pennaceus*. Most of the capsules in the cluster underwent no further change and the observations were terminated.

The egg mass collected at Hauula, Oahu (Table 1) (with an adult female, no. 1811, 35 × 21 mm.) was attached to the underside of a basalt rock in less than 0.5 m. of water. On the day of collection, one capsule was removed from the cluster and found to contain larvae in the advanced veliger or veliconcha stage. The latter term was introduced (Lamy, 1933; Werner, 1939) for fully developed veligers immediately prior to metamorphosis. The larval shells were pale orange pink and measured 1.2–1.3 × 0.7 mm. When released from the capsule, the larvae swam with the velar lobes up, a position apparently determined by the weight of the shell. The larvae closely resembled that illustrated by Ostergaard (1950: fig. 11e). The remaining intact capsules were placed in a vessel of slowly circulating aerated sea water and a substratum of sand from the reef.

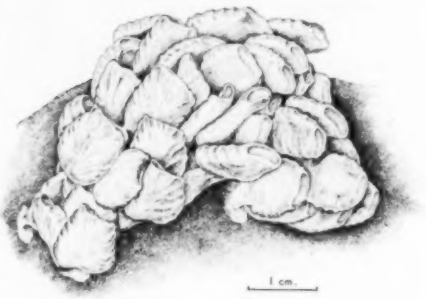

FIG. 8. Egg mass of *Conus pennaceus* Born. Diamond Head, Oahu, 10 June 1956.

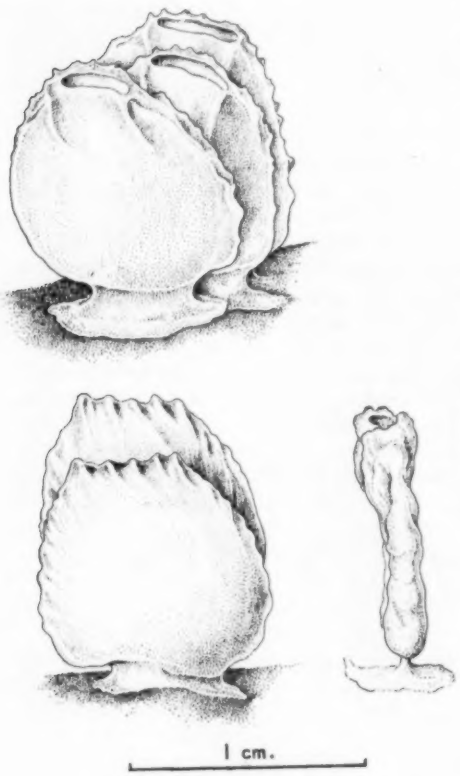

FIG. 7. Views of egg capsules tentatively assigned to *Conus lividus* Hwass *in* Bruguière. Maile, Oahu, 7 February 1956.

On the following day, one larva hatched from an egg capsule and, in contrast with those observed by Ostergaard, was quite able to swim about in the dish. However, its velar lobes and shell aperture always pointed upward, and the shell often rested on the substratum. The foot was not employed in locomotion. On the next day, 10 similar free-swimming veliconchas were observed in the dish. Two days later, although larvae remained in some capsules, many had hatched. A sample of these was observed to be distributed in the container as follows:

Freely swimming	0
Resting on bottom with velar lobes extended	
Velar lobes apparently regressing	3
Settled: crawling on substratum	38
Dead: empty shells	1
Sample size	79

The later stages of larval development in *C. pennaceus* may be summarized as follows: the larvae hatch as veliconchas which may swim

freely for about 1 day. They then rest on the bottom with the velar lobes extended upward and the cilia beating. Ostergaard's observation of propulsion along the substratum by the velar cilia was confirmed. Then the velar lobes begin to be resorbed. This was observed in three larvae, in which the margins of the velum were wrinkled and the length and width of the lobes was about one-half of the earlier dimensions. These veliconchas appeared otherwise normal. On the 2nd day after hatching, the young snail begins to crawl about on its foot (Fig. 10). However, the velar lobes have not been completely resorbed by this time; they are often extended by the crawling snail. When the larva assumes the benthic mode of life, the shell becomes darker orange in color, probably due to thickening, and new shell growth is apparent along the outer lip.

Ten days after the first hatching, the shells of the largest individuals measured 1.38 × 0.80 mm. and consisted of two complete whorls. However, mortality gradually increased in the culture, no individuals advanced beyond the end of the second whorl, and on the 27th day after the first hatching only one individual remained alive and the observations were terminated. Postlarval growth of *C. pennaceus* has been discussed elsewhere (Kohn, 1959*b*).

Conus quercinus Solander

Two clusters of egg capsules of *Conus quercinus* were collected in 1–2 m. of water at Sand (Ahuolaka) Island in Kaneohe Bay, Oahu, on 9 February 1956. The larger cluster contained 40 capsules and was affixed to a large clump of the red alga, *Acanthophora orientalis* J. Agardh.

FIG. 9. Views of an egg capsule of *Conus pennaceus* Born. Diamond Head, Oahu, 10 June 1956.

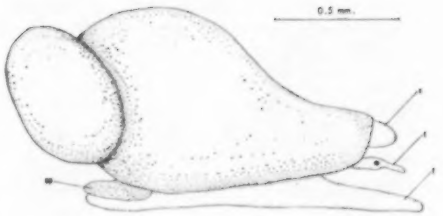

FIG. 10. Settled veliconcha of *Conus pennaceus* Born. *f*, Foot; *op*, operculum; *s*, siphon; *t*, tentacle, bearing the eye.

A pair of adult *Conus quercinus* (no. 1284, ♀, 91 × 56 mm.; no. 1285, ♂) were adjacent to the egg mass, and another pair and three single individuals were present within a radius of 1 m. *C. quercinus* appears to migrate from deeper water and to congregate for spawning in February–April of each year (Kohn, 1959*b*: 81). At this season adults are commonly found in the shallow water around Sand Island, a sand bank which is partially exposed at low tide. At other seasons they are absent from this site (Kohn, 1959*b*: fig. 29). The microhabitat of *C. quercinus* is quite distinct from those of its congeners in Hawaii (Kohn, 1959*b*). It occurs on vast sandy areas generally devoid of coral and rocks. As noted above, the egg capsules in the large mass were anchored to an alga. The other egg mass, which consisted of only three capsules, was affixed to a red sponge.

The congregation of several or many individuals associated with spawning was not observed in any other Hawaiian species of *Conus* but has been observed in other areas and will be discussed more fully elsewhere (Kohn, MS).

Most of the capsules in the large cluster were arranged in rows of up to eight and were affixed to each other by confluence of the basal plates (Fig. 11) as well as to the alga. A few were attached to previously deposited capsules, but this was not as common as in *C. pennaceus* and no bridges were present. The form of the capsules is rather irregular (Fig. 11). One wall bears numerous small ridges; the other has two more distinct ridges proceeding downward from near the corners of the exit window. The capsule is white when deposited but, since the

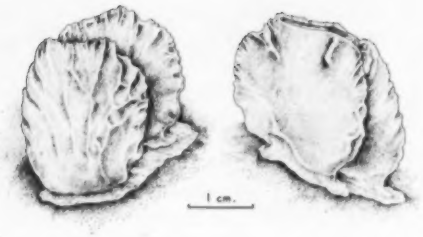

FIG. 11. Portion of a row of egg capsules of *Conus quercinus* Solander. Sand Island, Kaneohe Bay, Oahu, 9 February 1956.

cluster extends upward into the water and is not covered, it soon becomes a substratum for epiflora and epifauna. The characteristics of the egg masses of *C. quercinus* are summarized in Tables 1 and 2.

On the day of collection, one capsule was removed from the large cluster and found to contain pale pink, uncleaved, round-to-ovate eggs embedded in albuminous material and measuring 175–250 μ (Fig. 12*a*). The egg mass had probably been deposited on the same day. On the following day the first cleavage furrow was visible (Fig. 12*b*). On the 3rd day after collection, it was difficult to discern cell outlines, but the embryos, which were now white, appeared to be in the second to fourth divisions (Fig. 12*c, d*) and were motile when released from the capsule into sea water. Another capsule examined on the 5th day after collection showed little further progress. The embryos were quite motile and micromeres were observed in a few. Two days later, the embryos had increased in size to 240 $\times$ 180 μ and were in the modified trochophore stage (Fig. 12*e*).

Two days later, on the 9th day after oviposition, the embryos had grown to a maximum size of 315 $\times$ 195 μ and the shell and velar lobes had begun to form (Fig. 12*f*). Two days later, the fully developed veliger shells had attained a length of 255–295 μ. The velar lobes were well developed, and the heart, kidney (which was bright red), otocysts, eyes, and mouth (which measured 6 $\times$ 23 μ) were visible (Fig. 12*g, h, i*). The small foot rudiment bore a large operculum. The shell was brown and decorated with many rows of brown nodules, which were about 3 μ in diameter, rose 3–4 μ above the surface of the shell, and were about 3 μ apart. The growing lip of the shell was transparent.

On the 13th day after oviposition, the veligers were motile within the capsules and in many they were crowded in the vicinity of the exit window. Veligers removed from one capsule were found to have a row of green pigment spots, about 15 μ in diameter, inside the margins of the velar lobes, which had grown to about 285 μ across. The shells had not increased in size, but the outer lip was no longer transparent, indicating increased thickness. Two days later, on the 15th day after oviposition, some veligers hatched from the capsules and were swimming actively about in the container. By the following day most, and on the next day all, of the capsules had hatched.

Although the foot increased in size during the next few days, no significant over-all growth was apparent, and the velar lobes of some hatched veligers appeared reduced in size (Fig. 12*j*). None of the larvae settled to crawl on the bottom. Mortality in the culture gradually increased and only one or two larvae remained alive on the 8th day after the first hatching, when the observations were terminated.

Conus rattus Hwass *in* Bruguière (?)

A cluster of 31 egg capsules was collected from depressions in the underside of a large coral rock in 1 m. of water on the reef opposite the marine laboratory at Waikiki, Oahu, on 21 March 1956. No adult *Conus* was present in the immediate vicinity, but the capsules closely resemble those of *C. rattus* described by Ostergaard (1950).[4] They are tentatively assigned to that species, which is not uncommon on the same reef.

The capsules (Fig. 13) measured 11–15 $\times$ 10–14 mm. and most were empty. However, a few contained veliger larvae, which hatched soon after being placed in a vessel of sea water in the laboratory. The veliger shells were yellowish brown with darker brown granulations and measured 240 μ in maximum dimension. Eyes and otocysts were visible and a row of green pigment spots was present around the margins of the velar lobe. A few of the larvae remained

[4] This species is referred to as *C. tahitensis rattus* Hwass by Ostergaard (1950).

alive for 13 days after hatching, but they grew only to a length of 250 μ and no further development occurred.

Conus vitulinus Hwass *in* Bruguière

On 7 July 1956, at the reef at Ala Moana, Oahu, an adult *C. vitulinus* (no. 2020, 67 × 38 mm., sex undet.) was collected on sand under a dead coral rock, to the underside of which was attached an irregular cluster of 11 egg capsules. Some of the capsules were attached to others by confluence of the basal plates, but all were affixed to the substratum as well. They measured 23 × 16–17 mm. and their shape was typical of the genus (Fig. 14).

Eight hr. after collection, one capsule was examined and found to contain 1-, 2-, and 4-cell stages, which measured 225 μ in diameter

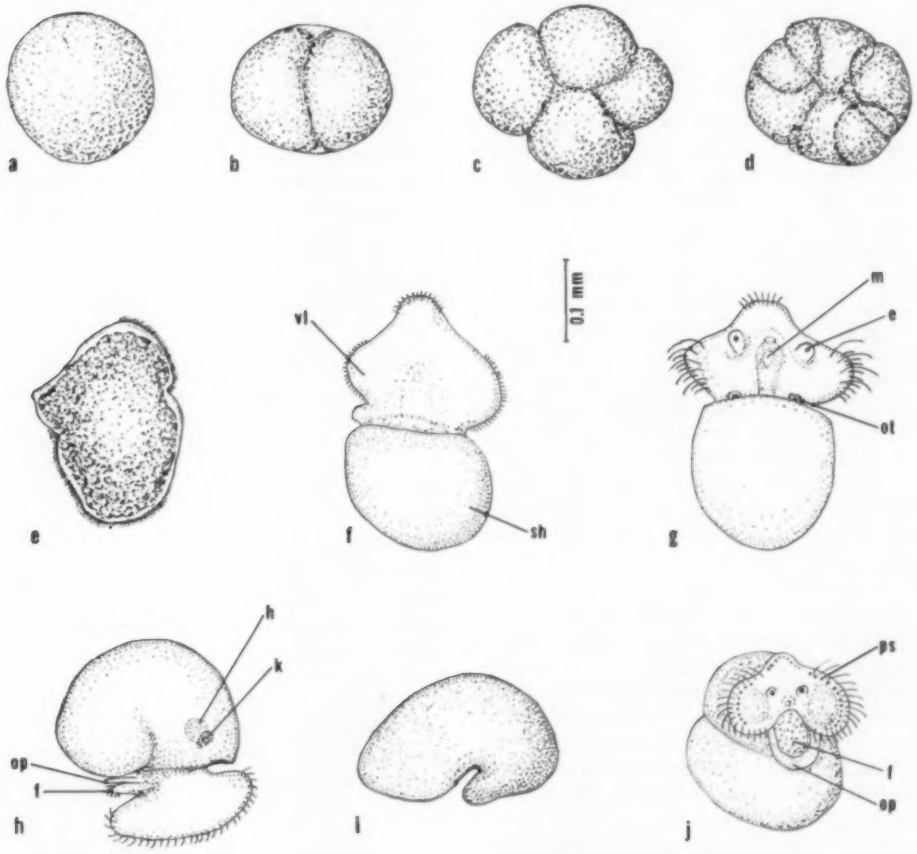

FIG. 12. Developmental stages of *Conus quercinus* Solander, from the same egg mass as the capsules illustrated in Figure 11. *a*, Uncleaved egg; *b*, 2-cell stage; *c*, 4-cell stage; *d*, embryo in third cleavage division; *e*, trochophore-like stage; *f*, early veliger; *g*, developing veliger, anterior-ventral view; *h*, developing veliger, right lateral view; *i*, shell of veliger, left lateral view; *j*, hatched, fully developed veliger. *e*, Eye; *f*, foot; *h*, heart; *k*, kidney; *m*, mouth; *op*, operculum; *ot*, otocyst; *ps*, pigment spots; *sh*, shell; *vl*, velar lobe. Nodules present on shells are not indicated in figures.

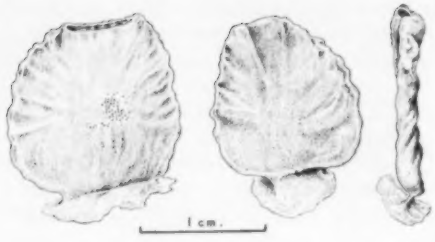

FIG. 13. Views of an egg capsule tentatively assigned to *Conus rattus* Hwass *in* Bruguière. Waikiki, Oahu, 21 March 1956.

(Fig. 15*a*, *b*). Oviposition probably occurred earlier the same day. Two days later, the embryos had progressed to the early blastula stage and macromeres and micromeres were distinctly visible (Fig. 15*c*). A capsule examined on the 6th day after collection was found to contain motile trochophore-like larvae which measured 360 × 210 μ (Fig. 15*d*). On the 9th day, the veliger stage was fully developed, the maximum dimension being 375–400 μ (Fig. 15*e*, *f*). On the 11th day, the veligers were motile within the capsules and on the following day crowding toward the exit window was observed. All of the capsules hatched during the next 3 days, or 14–16 days after oviposition. The otocysts and reddish-brown kidney were visible and green pigment spots almost filled the velar lobes of some individuals.

Some of the veligers swam about freely in the vessel, but most remained on the bottom, which had been covered with sand from the reef, and propelled themselves by beating the velar cilia. When disturbed, they swam briefly away from the source of irritation. However, none of the larvae settled to crawl on their feet, and all had died without undergoing any further growth or development by the 4th day after hatching began.

On 24 July 1957, a cluster of 12 egg capsules was found attached to the underside of a coral rock in a large tide pool at Diamond Head, Oahu. A large adult *C. vitulinus* (no. 7034, 65 × 37 mm., sex undet.) was present on the sand substratum under the rock. Upon return to the laboratory, one of the capsules was examined and found to contain eggs in 1-, 2-, and 4-cell stages; the last measured about 250 μ across. On the second day after collection, a capsule contained embryos which still measured 250 μ in diameter but had progressed to the blastula stage. The observations had to be terminated at this point, but development thus far was essentially similar to that in the egg mass described above.

DISCUSSION

Spawning site and season. Egg capsules of *Conus* have been collected on 31 known occasions in Hawaii, chiefly by Ostergaard (1950) and by the writer and colleagues. All collection records are summarized in Table 1. At least 12 species are represented.

As noted previously (Kohn, 1959*b*):

> Coral reef platforms, but not marine benches, provide suitable attachment sites for egg capsules of *Conus*. Of 36 egg masses collected in the field, 29 were recorded from reef platforms. An almost complete absence of records from marine benches suggests that spawning is unsuccessful there. This is probably due to the absence of protected pools in which egg capsules may be deposited without being subject to desiccation at low tide and/or torn away by heavy surf at high tide. Recruitment of bench populations [of adults] is probably from pelagic veliger larvae which have been carried from other areas and are washed onto marine benches in condition to settle and assume the benthic mode of life.

All of the capsules were collected between February and August, although search for them was not restricted to, or emphasized during, that period. The data suggest that most species of

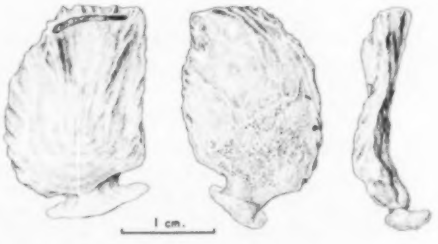

FIG. 14. Views of an egg capsule of *Conus vitulinus* Hwass in Bruguière. Ala Moana, Oahu, 7 July 1956.

Conus spawn during about the same part of the year. The spawning season of most species for which more than one egg mass has been collected is rather extended over the months cited. Capsules containing viable eggs and embryos of *C. rattus* have been collected from February to August, of *C. abbreviatus* from March to July, and of *C. pennaceus* from May to August.

The spawn of most species has been observed only rarely. However, 12 egg masses of *Conus pennaceus* were collected on nine occasions, all in the months of May, June, July, and August, suggesting that these months constitute the breeding season in this species. The preponderance of data for *C. pennaceus* (Table 1) is attributed partly to the fact that the egg masses of this species are readily identifiable, even in the absence of the parent from the collection site. Unlike other species, which attach each capsule to the substratum, *C. pennaceus* attaches only a few to the substratum, while the rest are attached to previously deposited capsules.

Development. The eggs of *Conus* are typically white or pink, spherical or nearly so, and without a surrounding membrane. Polar bodies were not observed, but Ostergaard (1950) reported their occurrence in *C. vexillum*.[5] There are no nurse eggs; all or almost all eggs may develop to hatching in nature, but development was often arrested in a usually small but variable proportion of embryos in egg masses cultured in the laboratory.

The number of eggs produced, egg diameter, length of development before hatching, and stage at hatching are summarized for 11 species of *Conus* from Hawaii in Table 2. Egg diameter was measured in 8 species, of which 7 ranged from 125 μ to 225 μ. In all of these species, the number of eggs was large, about 1,000–10,000 per egg capsule and 15,000–210,000 per egg mass (Table 2). One species, *C. pennaceus*, has much larger eggs (460 μ), of which considerably fewer are deposited (80/egg capsule; 3,500/egg mass).

As can be seen in Table 2, all the species with large numbers of small eggs hatch as free-swimming veligers, while *C. pennaceus* has virtually no pelagic stage, as was discussed in detail above. These data are in agreement with the correlations of large numbers of small eggs with long pelagic life and small numbers of large eggs with nonpelagic development first demonstrated by Thorson (1950, 1952) for mollusks and other benthic marine invertebrates.

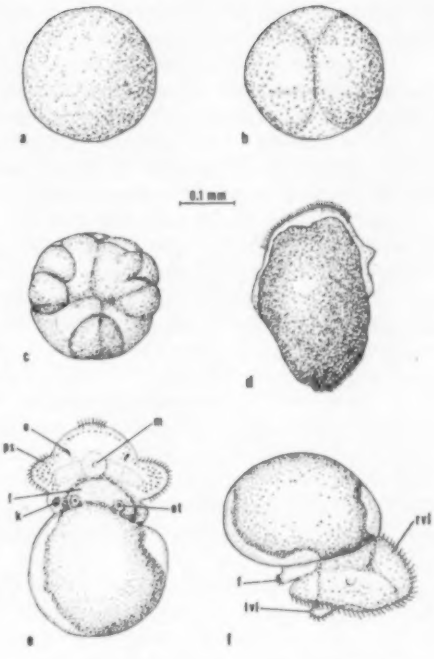

FIG. 15. Developmental stages of *Conus vitulinus* Hwass *in* Bruguière, from the same egg mass as the capsule illustrated in Figure 14. *a*, Uncleaved egg; *b*, 2-cell stage; *c*, early blastula; *d*, trochophore-like stage; *e*, veliger, anterior-ventral view; *f*, veliger, lateral view. *e*, Eye; *f*, foot; *k*, kidney; *lvl*, left velar lobe; *m*, mouth; *ot*, otocyst; *ps*, pigment spot; *rvl*, right velar lobe.

Salient features of development in four species of *Conus* are summarized in Table 3. The eggs are fertilized but have not yet undergone first cleavage when enclosed in the egg capsules. In the species studied, the trochophore stage is entered at 2–6 days, and the veliger stage at 6–10 days, after spawning. Larvae hatch as veligers about 2 weeks after spawning. These observations are in agreement with those of Ostergaard (1950), who also reported on development in

[5] This species is referred to as *C. sumatrensis* Hwass by Ostergaard (1950).

four other species, which hatched 12–16 days after spawning.

In laboratory cultures, many of the veligers (up to 75 per cent) did not succeed in escaping from the capsules. However, this may have been due to the abnormal spatial position of the detached capsules; it is less likely to occur in nature. It has been noted above that the capsules are usually affixed to the underside of a rock. Since the exit window is thus oriented downward in nature, escape of the larvae from the capsule may be facilitated by gravity after disappearance of the membrane covering the exit window. However, in laboratory cultures in which capsules were oriented as shown in Figure 1, larvae ready to hatch were often observed crowded toward the exit window before dissolution of the membrane, and many escaped from the capsule by actively swimming upward. These observations suggest that positive or negative geotropism is not a factor in the hatching of *Conus* larvae.

The length of the pelagic stage could not be determined except for *C. pennaceus*, in which it is only 1 day or less. The maximum survival time of free-swimming veligers in the writer's laboratory was 13 days (*C. rattus*). Partial metamorphosis was observed only in *C. pennaceus*.

The nature of the food of the larval stages is unknown. Protozoa abounded in the cultures. Thorson (1946) concluded that all prosobranch larvae known from the Øresund feed on phytoplankton, and he calculated the theoretical maximum diameter of the food to be 5–45 μ. The mouths of *Conus* veligers measured were of about the same diameter as the esophagus of the smaller larvae measured by Thorson. Thus the larvae of *Conus* probably depend for food on phytoplankton, nannoplankton, and detritus. Examination of squash preparations of *C. pennaceus* a few days after settling revealed the presence of radula teeth. These differ in form from the adult teeth, being shorter in proportion to the thickness, and they are probably not functional. The method of feeding, as well as the food, is thus not known at this stage of the life history. The rather fragmentary information available on post-larval development and growth of *Conus* in Hawaii has been reported elsewhere (Kohn, 1959*b*).

SUMMARY

Egg capsules of 9 of the 33 species of *Conus* found in Hawaii are described and figured. Interspecific variation is usually not sufficient to permit identification of the species to which an egg mass belongs in the absence of the parent.

The complete course of larval development within the egg capsule from spawning (uncleaved egg) to hatching (veliger or veliconcha) is described for 4 species. Early cleavage stages occur 1–3 days after spawning, suppressed trochophore stage at 2–6 days, and veliger stage at 6–10 days. Freely swimming veligers hatched from egg capsules of 3 species 14–15 days after oviposition, in agreement with the developmental time scale of other species of *Conus* previously reported on by Ostergaard (1950).

All species found to have pelagic larval stages produced large numbers (15,000–210,000) of small (125–225 μ) eggs. It was not possible to determine the length of the free-swimming stage in any of these species.

Hatching in one species, *C. pennaceus*, occurs 16–26 days after oviposition at the advanced veliger or veliconcha stage. The larvae swim about for 1 day or less and then assume the benthic habit and begin metamorphosis. This species produces small numbers (3,500) of large (460 μ) eggs. This characteristic is correlated with the absence of a long pelagic larval stage.

ACKNOWLEDGMENTS

This study was aided by a grant from the Sigma Xi–RESA Research Fund, 1959. It was carried out at the Hawaii Marine Laboratory of the University of Hawaii and the Marine Biological Laboratory of the University of Copenhagen. The writer is extremely grateful to Prof. Gunnar Thorson for providing laboratory facilities at the latter institution, access to unpublished data, and stimulating discussions, and for arranging for the services of Mr. P. H. Winther, who drew Figures 2, 4–9, 11, 13, and 14. The other figures were prepared by the author from sketches of living specimens and from camera lucida drawings of fixed material. Appreciation is also expressed to the staffs of the two laboratories mentioned above for much helpful assistance.

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Revision of the Genus *Pandanus* Stickman, Part 2
Pandanus in Western Australia and Notes on the Section Foullioya

HAROLD ST. JOHN[1]

THIS IS THE SECOND PART of a revision of the genus *Pandanus*. The previous one was printed in *Pacific Science* 14(3): 224–241, 1960.

There have been earlier printed reports of *Pandanus* occurring in the state of Western Australia. These all identified the species as ones native to distant areas. The existing specimens from the region are meager, but by examining them in all of the principal Australian herbaria it has been possible to learn enough of their structure to classify two of them. There are indications of a third species, but the two following are sufficiently known. As they appear to be novelties, they are here described as new species.

Pandanus kimberleyanus sp. nov. (sect. *Microstigma*)
Fig. 9

DIAGNOSIS HOLOTYPI: Arbor? "12–25 ped. alt.," gracilis cum radicibus aereis; *foliis* 1.29 m. longis 6.2 cm. latis prope basi sed 3–7 cm. latis prope medio longe acuminatis circa 10 cm. ex apice 6 mm. latis firmis valde fibrosis marginibus in basi inermibus sed in tertia infera armatis dentibus 2–3 mm. longis subulatis brunneo-cacumenatis adscendentibus 2–13 mm. distantibus sed in tertia medialis in uno latere inermibus et in altero latere cum dentibus simulantibus 9–17 mm. distantibus sed in parte apicali dentibus adscendentibus 0.2–0.5 mm. longis 3–7 mm. distantibus, nervo medio inermi, *inflorescentia* foeminea solitaria et terminali (?), pedunculo 19 cm. longo 7–12 mm. diametro trigono, bracteis numerosis foliosis ad 95 cm. longis 10–14 mm. latis longe acuminatis et subulatis, syncarpio 10 cm. longo 7.5 cm. diametro ovoideo obtuse subtrigono, *drupis* 2.5–2.8 cm. longis 1.2–1.3 cm. latis 1 cm. diametro in basi 5–10 mm. latis, corpore anguste obovoideo coloribus incognitis in sicco epidermatibus exfoliatis fibris longitudinalibus numerosis nudatis, caverna apicali parte cum tubera brunnea cumpleta, stigmate 2 mm. lata anguste lunata excentrale in margine sentinae apicale, endocarpio minime submediale osseoso obscure brunneo muris externis 1.5 mm. crassis, seminibus 7 × 5.5 mm., mesocarpio apicalis caverno singulo, mesocarpio basilari carnoso et valide fibroso.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree, "erect, 12–25 ft. high," slender and with prop roots; *leaves* 1.27–1.29 m. long, 6.2 cm. wide near the base, 3.7–6.1 cm. wide near the middle, long tapering to a slender, narrowing tip, the actual tip (probably about 3 cm. long and 2 mm. wide) is missing, and at about 10 cm. from the tip it is only 6 mm. wide, texture firm, with strong fibrous veins; the margins unarmed for the lower 8 cm., on the lower third the margins with ascending brown-tipped, subulate teeth 2–3 mm. long, 2–13 mm. apart, at the middle unarmed on one margin, but on the other with similar teeth, appressed and 9–17 mm. apart, near the apex the teeth ascending, 0.2–0.5 mm. long, 3–7 mm. apart, midrib unarmed; *pistillate inflorescence* single and apparently terminal; peduncle 19–20.5 cm. long, 7–12 mm. in diameter, trigonous, with numerous leafy bracts up to 95 cm. long, 10–14 mm. wide, long tapering to a subulate tip; *syncarp* 10 cm. long, 7.5 cm. in diameter, ovoid, obtusely subtrigonous, drupes about 140, crowded, the upper ¼ exposed; *drupes* 2.5–2.8 cm. long, 1.2–1.3 cm. wide, 1 cm. thick, the base 5–10 mm. wide, the body narrowly obovoid, color not recorded, on drying the smooth epidermis exfoliating and exposing the numerous longitudinal fibers, apical concavity partly filled by a darker brown, pillow-

[1] B. P. Bishop Museum, Honolulu 17, Hawaii. Manuscript received December 12, 1959.

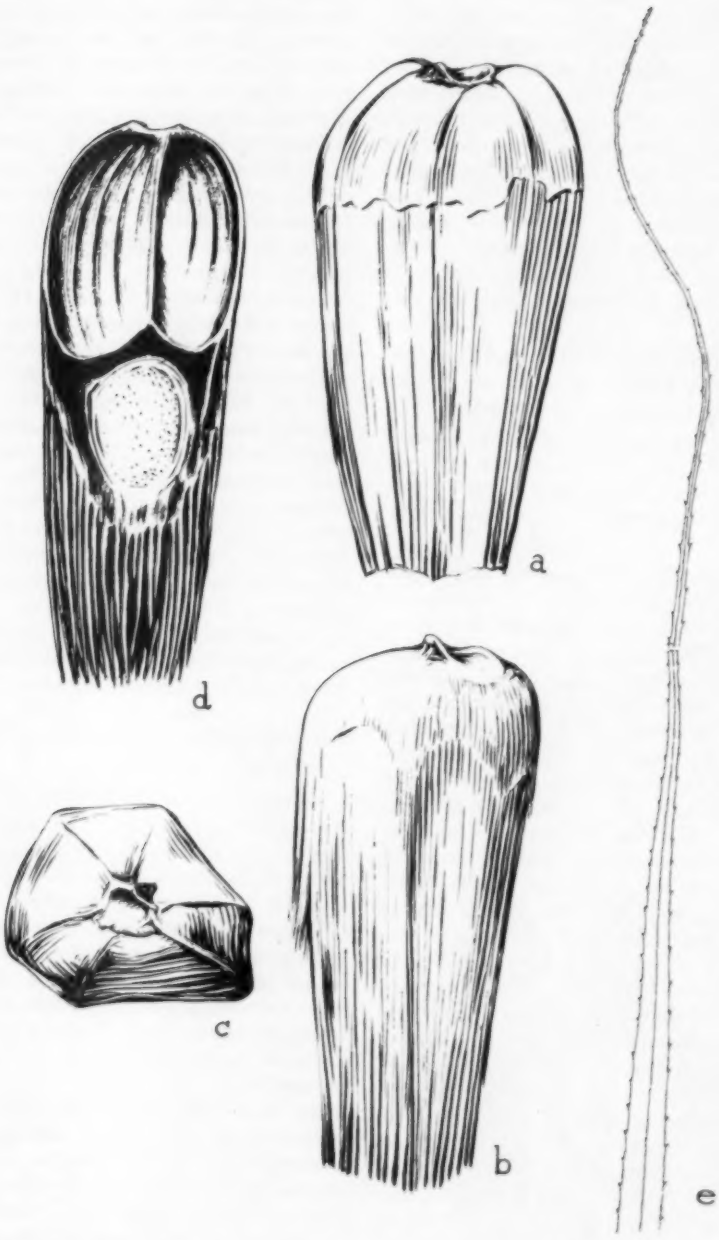

FIG. 9. *Pandanus kimberleyanus* St. John, from holotype. *a, b, c, d,* Drupe × 2⅔; *e,* leaf tip × ⅔.

like swelling; stigma 2 mm. wide, narrow lunate, on the margin of the concavity, excentric; endocarp slightly submedian, dark brown, bony, the outer wall 1.5 mm. thick; seed cavity 7 × 5.5 mm.; apical mesocarp one large cavity; basal mesocarp fleshy and strongly fibrous; *staminate inflorescence* leafy bracts almost unarmed; tip of inflorescence 4.5 cm. long, lateral spikes 1.5–2.5 cm. long; staminal columns 4–7 mm. long, stout, antheriferous in upper third, bearing about 7 anthers, free filament tips 0.3–1.3 mm. long; anthers 1.8–2 mm. long, 0.3 mm. wide, narrowly oblong, the base subsagittate, the apex apiculate.

HOLOTYPUS: Western Australia, West Kimberley, Fitzroy River, Aug. 1906, *W. V. Fitzgerald 2,395,* fruiting specimen, (NSW).

SPECIMENS EXAMINED: Western Australia, West Kimberley, mixed with the holotype, but a staminate inflorescence (NSW); Denham River, Oct. 1906, *W. V. Fitzgerald 1,625* (PERTH).

DISCUSSION: The specimens here described as new have been identified as *P. aquaticus* F. Muell., which species was first published by von Mueller in 1856 as a provisional species. Later, in 1865, he accepted and validated it with a description which included no more than that the plants were small and slender, lacked aerial roots, and had separate drupes. Bentham received from von Mueller only leaves and a staminate inflorescence, so could not fully document the species. Warburg saw no more and considered the species dubious. Martelli mentioned no specimens but listed the species. Blake (1954: 131) considered it to be the same as, and an earlier name for, *P. de-Lestangii.* The type locality of *P. aquaticus* was upper Victoria River, Northern Territory, and that of *P. de-Lestangii* Martelli was Burketown, n. w. Queensland. Blake considered that there was only one such species in northern Australia, reduced *P. de-Lestangii* to synonymy, and accepted *P. aquaticus* as the correct name. The present writer found in the Melbourne herbarium *P. aquaticus* F. Muell., from upper Victoria River, Dec. 1955, F. v. Mueller. The specimen consists of only a single leaf. It seems to be the holotype or an isotype. The one at Kew is little better, and the description was inadequate. After much field experience, it is realized that numerous species may grow side by side, and that geographic proximity of collections is not enough basis for reducing taxa to synonymy in this genus. It seems better to concur with Bentham and with Warburg and to continue to place *P. aquaticus* F. Muell. with the imperfectly known species. *P. de-Lestangii* Martelli was adequately described and illustrated from fruiting material, and staminate material is also known. This species is known to occur from the Daly River, Northern Territory, to the Gregory River, northwest Queensland. Fitzgerald (1918: 110) treated this species as *P. aquaticus* in his check list. Besides the two localities from which specimens were seen, he also gave the additional localities: Isdell, Charnley, and King River.

P. de-Lestangii Martelli, of the section *Microstigma,* has drupes 3.5–4.3 mm. long, stigmas apical, oblique, suborbicular, 1–3 in number; syncarp 10–13 cm. in diameter; leaves 4.5–8 cm. wide. *P. kimberleyanus,* of the same section, has drupes 2.5–2.8 cm. long; stigma narrowly lunate, excentric on the margin of the apical concavity; and leaves 3.7 cm. wide.

The new specific epithet is a geographic adjective, made from the name of the well-known Kimberley district where the plant occurs.

Pandanus convexus sp. nov. (sect. *Pandanus*)
Fig. 10

DIAGNOSIS HOLOTYPI: Arbor 10 m. altus, *phalangibus* (unam vidi) 6.3 cm. longis 6.6 cm. latis 5.2 cm. crassis late cuneatis in basi truncatis, lateribus planis levibus lucidis parte tertia superiore libera, sinibus lateralibus inter carpellas plerumque tam longis quam parte libera, angulis lateralibus minoribus et paucis, apice alto-convexa, carpellis 8, apicibus carpellarum depresso-convexis, sinibus centralibus 1.5–3 mm. profundis, stigmatibus 4–5 mm. longis subcentralibus suborbicularibus centripetalibus cordatis horizontalibus, endocarpio submediali 47 mm. longo 54 mm. lato magno obscure brunneo osseoso, seminibus 16–17 mm. longis 4–4.5 mm. diametro ellipsoideo, mesocarpio apicali cum cavernis parvis remotis medullosis et cum fibris, mesocarpio basali minimi fibrosi et carnosi.

DESCRIPTION OF ALL SPECIMENS EXAMINED: Tree 10 m. tall; trunks usually several together,

bi- tri-furcated near the summit; leaves 1.7 m. long, 6.7 cm. wide, lance-ligulate, long tapering; the marginal teeth at base few and small; the median teeth 2–4 mm. long, 5–12 mm. apart, acicular, appressed ascending, the larger ones red brown at tip; the teeth near the apex 0.2–1 mm. long, 5–12 mm. apart; midrib below with strong, retrorse prickles 3–4 mm. long, 12–25 mm. apart, red brown; *syncarps* "6–9 in. in diam., globular, red," *phalanges* 5.9–6.3 cm. long, 6.6–7.9 cm. wide, 5.2–7.6 cm. thick, "red," broad cuneate, the base truncate, the sides plane, smooth, shining, upper ⅓ free, the lateral sutures between the carpels as long as or shorter than the upper free part, lateral angles few and low, apex high convex; carpels 8–9, each apex low convex and with a radial suture line from the sinus to the stigma; inner sinuses 1.5–3 mm. deep; stigmas 4–5 mm. long, nearly central, suborbicular cordate, horizontal, flush, centripetal; endocarp slightly submedian, 47 mm. long, 54 mm. wide, massive, bony, dark brown; seeds 16–17 mm. long, 4–4.5 mm. in diameter, ellipsoid; apical mesocarp with small remote caverns which have longitudinal fibers and pithy cross partitions; basal mesocarp very small, fibrous and fleshy; *staminate inflorescence* 15.5 cm. long, 3 cm. diam., compact ellipsoid, with bracts 3–6 dm. long, 2–2.5 cm. wide, foliaceous, the margins entire; lateral spikes 1.5–3 cm. long, dense; stamens racemose; *anthers* 4.5–6 mm. long, linear sagittate, acuminate.

HOLOTYPUS: Western Australia, Dillens Springs, Oct. 1906, *W. V. Fitzgerald 2,394* (SYD).

SPECIMENS EXAMINED: Western Australia, Dillens Springs, Oct. 1906, *W. V. Fitzgerald 2394* (the staminate inflorescence mixed with the holotype) (SYD).

Northern Territory: Escape Cliffs, *Hulls* [an error for *W. Hulse*] (Mel).

DISCUSSION: This species is known from meager collections, but it seems amply distinct by its phalanges with 8–9 carpels, small remote

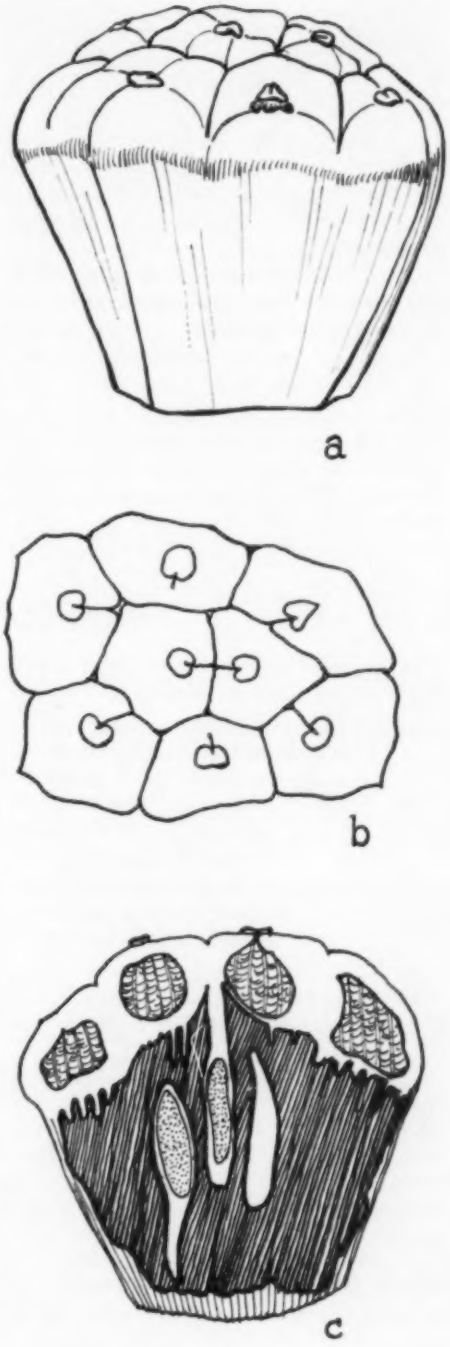

FIG. 10. *Pandanus convexus* St. John, from holotype. *a, b, c,* Phalange × 1.

apical mesocarp caverns, and the massive endocarp filling 5/6 of the interior. The related *P. spiralis* R. Br., described from the Wellesley Group, Gulf of Carpentaria, Queensland, has the phalanges with 16–22 carpels, the apical mesocarp caverns contiguous and ¼ as long as the phalange; and the endocarp ½ as long as the phalange and consisting of narrow, mostly separate bands.

The type locality is listed by Fitzgerald (1918: 220) as Dillen's Springs, spelled with an apostrophe. The locality is about 47 mi. south of Wyndham in East Kimberley and at approximately 16° S., 128° E.

The collector of the specimen from Escape Cliffs was published by Bentham (1878: 149) as Hulls. This was an error. The collector's name was really W. Hulse, as indicated by F. von Mueller (1869: 20).

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NOTES ON THE SECTION FOULLIOYA

In the preceding Part 1, the section Foullioya Warb. was listed but was omitted from the key. It should be inserted as follows, on p. 3, replace the second D, by:

D. Stigmas narrower than apex of drupe,
  a. Stigmas lunate, lateral under a horizontal coriaceous, entire or lobed visor borne asymmetrically on the apical region of the drupe but not marginal; syncarp solitary, cylindric, enwrapped in boat-shaped colored bracts; staminate flowers unknown ..... *Maysops*
  a. Stigmas deeply 2-lobed, tonguelike or reniform and 2-lobed, terminal, ascendings arcuate; syncarps several, globose to broad ellipsoid, with a single bract, exposed; stamens few, fascicled at apex of column ..... *Foullioya*

The genus *Fouilloya* Gaud., when published in 1841, contained illustrations of the two following species:

First, *F. maritima* Gaud. It was suggested by Brongniart (Ann. Sci. Nat. Bot. VI, 1: 291, 1875), that the type of this came from Madagascar or Mauritius. Later, Vaughan and Wiehe (Linn. Soc. Bot. J. 55: 20, 1953), report no living species on Mauritius that agrees with it and no evidence that it previously existed there. It has not been rediscovered elsewhere, but all its close relatives are native to Madagascar. It was renamed *Pandanus maritimus* Solms (1878), but this is a later homonym of *P. maritimus* Thouars (1808). So, this species has not been rediscovered since its publication in 1841, its homeland is unknown, and the specific epithet is unavailable in *Pandanus*.

Second, *F. racemosa* Gaud. Solely upon this was founded *Pandanus racemosus* Kurz (1869). It has not been rediscovered, and is known only from the Gaudichaud illustration and his specimen. Its homeland is unknown, but its relatives occur in Madagascar.

The group was first validly published as the section *Foullioya* (as *Fouilloya*) by Warburg

(1900), emend. Pic.-Ser. (1951). He included and accepted the two species first announced by Gaudichaud (1841) and added the two following:

P. Boivini Solms (1878) was described from a staminate flowering specimen, collected in Madagascar. The pistillate material for this species has not yet been discovered.

P. pygmaeus Thouars (1808), a Madagascar species represented by several recent collections, and by illustrations.

In choosing a lectotype one would normally prefer one of the two species that Gaudichaud included when he originally published the group as a genus. But, both of these are known only by the figures of the fruit given by Gaudichaud and by his scanty type specimens at Paris, and their nativity is unknown. Either of them would be unsatisfactory as a type. Consequently, depending on the fact that the genus when published by Gaudichaud was bitypic, and was without description, and was thus invalid, it is permissible to bypass them. Of the four original species in the valid section *Foullioya* Warb. emend. Pic.-Ser., only one is well known, of known origin, and still extant. Consequently this species is here chosen as, lectotype: *P. pygmaeus* Thouars.

Errata

The drawings for St. John's "Revision of the Genus *Pandanus* Stickman, Part 1," which appeared in Pacific Science 14(3): 224–241, were reduced to sizes which did not agree with the measures indicated in the legends.

Newly-written legends, which correct the errors, are presented herewith.

FIG. 1. *Pandanus biakensis*, from the holotype. *a*, Leaf base underside, × 5/11; *b*, leaf base margin, × 1.8; *c*, leaf middle underside, × 5/11; *d*, leaf tip underside, × 5/11; *e*, phalange, lateral view, × 5/11; *f*, phalange, longitudinal median section, × 5/11; *g*, phalange apex, × 1.8.

FIG. 6. *Pandanus conicus*, holotype. *a*, Phalange, lateral view, × ¾; *b*, phalange, longitudinal median section, × ¾; *c*, phalange, apical view, × ¾; *d*, carpel apices and stigmas, an inner one at lower right, and three outer ones, oblique view, × 3; *e*, leaf base, lower side, × ¾; *f*, leaf middle, lower side, × ¾; *g*, leaf tip, lower side, × ¾; *h*, leaf tip, lateral view, × ¾; *i*, leaf tip, lateral view, × 3.

FIG. 7. *Pandanus cochleatus*, from holotype. *a*, Phalange, lateral view, × ¾; *b*, phalange, longitudinal median section, × ¾; *c*, phalange, apical view, × ¾; *d*, carpel apices and stigmas, an inner one at left, and two outer ones, oblique view, × 3; *e*, leaf base, lower side, × ¾; *f*, leaf middle, lower side, × ¾; *g*, leaf margin at middle, × 3; *h*, leaf apex, lower side, × ¾.

FIG. 8. *Pandanus Zea*, holotype. *a*, Younger syncarp, × 3/14; *b*, mature syncarp, × 3/14; *c*, lateral drupes from above, × ¾; *d,e*, lateral drupes, from above, × 3; *f*, lateral drupe from side, × 3; *g*, lateral drupe from side, × ¾; *h*, lateral drupe from side, × 3; *i*, lateral drupe, longitudinal median section, × 3; *j*, apical drupes, from above, × ¾; *k,l*, apical drupes, from above, × 3; *m*, apical drupe, oblique lateral view, × 3; *n*, apical drupe, lateral view, × ¾; *o*, apical drupe, lateral view, × 3; *p*, apical drupe, longitudinal median section, × 3; *q*, leaf base, lower side, × ¾; *r*, leaf middle, lower side, × ¾; *s*, leaf apex, lower side, × ¾.

Fungi from Raroia in the Tuamotu Archipelago

WILLIAM BRIDGE COOKE[1]

BETWEEN July 21 and September 6, 1952, M. S. Doty collected a number of specimens of fungi on Raroia (ca. 16°05′ S., 142°25′ W.) in the Tuamotu Archipelago. These were sent to the writer for identification. In turn, certain specimens were forwarded to specialists for more accurate identification than the writer could furnish.

The geographic distribution of the fungi of the islands in the Pacific Ocean is poorly known, largely because usually only the more obvious things, such as *Pycnoporus sanguineus,* are collected. It is probable that the fungi of the Tuamotus have never before been collected as thoroughly as they were on Dr. Doty's visit.

There are few habitats on an atoll for fungi. These are largely the dead wood of native or introduced trees, and driftwood.

In addition to the seven species reported below, based on material in 19 collections, other species were found. However, some specimens were unidentified because they were immature at the time of collection, had passed maturity and were no longer producing spores, or were poorly dried because of inadequate drying facilities.

The writer wishes to acknowledge the help of B. Lowy, J. H. Miller, L. E. Wehmeyer, John Eriksson, S. J. Hughes, J. A. Stevenson, and J. L. Lowe, in identifying this material. Duplicate specimens of all species listed have been forwarded to the Bishop Museum, Honolulu; and the National Fungus Collections, Beltsville, Maryland. Duplicates of several species were sent to the New York Botanical Gardens.

ASCOMYCETES

Anthostomella sp.

On fallen rachis of leaf of *Cocos nucifera.* 11274, 11277. July 21, 1952. 11277 is older than 11274 and has more crowded perithecia. Dr. L. E. Wehmeyer stated that these specimens have the spores of *A. melanosticta* but that this species shows no surface blackening. Additional species which are similar include *A. contaminans* (Dur. & Mont.) Sacc., and *A. lugubris* (Rob. & Desm.) Sacc. The description of *A. cocoes-capitatae* Cab. was not available at the time of examination.

Hypoxylon chrysoconium Berk. & Br.

Six collections were made from decaying wood of *Guettarda speciosa* or *Messerschmidia argentea.* 11279, 11280, 11374, 11389, 11390, 11393. July 21, 28, 29. Dr. J. H. Miller stated that "this is intermediate with *Rosellinia* but the perithecia are often united into an effused stroma. It occurs from India through the Hawaiian Islands." The mycelium on the surface of the wood is golden in color, making the species readily identifiable in the field. Two specimens were without perithecia and so were identified by analogy.

Hypoxylon investiens (Schw.) Berk.

Three specimens were obtained from decaying wood of *Guettarda speciosa* or *Messerschmidia argentea.* 11267, 11273, 11606. July 21, August 7. Dr. Miller indicated that the specimens were rather old, showed few perithecia, and that blackening of the wood was characteristic of the species. This species forms thin, brown, effused patches on decaying twigs, branches, and wood.

Phaeopeltosphaeria irregularis Wehmeyer

Two specimens of this species were found on old wood, probably drift wood. 11164, 11394. July 9, 28. Dr. Wehmeyer indicated that this species has now been found on three atolls of the Marshall Islands and on the Galapagos Islands. He said that "it is apparently common in the South Pacific on driftwood."

[1] Robert A. Taft Sanitary Engineering Center, Bureau of State Services, Public Health Service, U. S. Department of Health, Education, and Welfare, Cincinnati, Ohio. Manuscript received January 18, 1960.

BASIDIOMYCETES

Auricularia mesenterica Pers.

Three collections of this widely distributed tropical species were taken from wood of *Messerschmidia argentea*. 11262, 11386, 11661. July 21, 28, August 8.

Schizophyllum commune Fr.

Although the shape of the specimens obtained by Doty is typical of more northern material usually assigned to this species, this specimen could as easily have been placed in *S. radiatum* (Swartz) Fries[2] because of its tropical distribution. Throughout the Pacific Basin only one species is recognized in this genus at present. 11425. July 26.

Thirteen collections of thelephoraceous fungi were sent to John Eriksson for identification. Unfortunately, Dr. Eriksson was unfamiliar with the species these collections represent. In addition, the methods of preservation of these specimens make their identification quite difficult. Representatives of *Peniophora* sect. *Coloratae*, and sect. *Hyphales* were present. No spores and no fertile fruiting structures were present in the collections, although in some cases holobasidia were observable. It was suggested that through habitat, knowledge of sterile hymenial structures, and other features of a collection, a person familiar with tropical species in this group could make tentative identifications.

The same difficulties were found in the several collections of pore fungi which were made. A large trametoid specimen, a medium-size black *Phellinus*-like species represented by two normal specimens and two overgrown with a *Peniophora*-like species, and nine specimens of resupinate polypores were among the materials obtained. Because of his wide familiarity with tropical polypores these specimens were submitted to John A. Stevenson, National Fungus Collections, for study. The writer had found no satisfactory basidial or spore characters and hoped that sight identification might be possible. Neither Mr. Stevenson, nor Josiah L. Lowe who also examined them, could come to any conclusion concerning species names for these specimens.

The collection and adequate preparation of specimens of this type in tropical regions is difficult. It has been suggested that if quick drying equipment is not readily available, the hymenia should be inverted to prevent loss of spores during drying. Care should also be taken to prevent the specimens from getting too wet during periods of prolonged rain or high humidity. This condition tends to reactivate the hymenial tissues and exhaust the spore-producing capacity of the basidia, which then become unrecognizable structures.

FUNGI IMPERFECTI

Helicomyces roseus Link

Two specimens composed of pieces of wood partially covered with a white effused growth were assigned to this species. Spores from this white growth were very similar to those described by Linder (Ann. Mo. Bot. Gard. 16: 271, 1929) for this species. The material was assigned to this species on that basis as well as on the fact that it resembles closely material described under this name by Rogers (Pacif. Sci. 1: 106, 1947), from the Marshall Islands. Dr. S. J. Hughes did not agree with this identification but offered no substitute. 11283, 11602. July 21, September 6.

Helicosporium lumbricoides Sacc. em. Matr.

Two collections were made from material on old spathes of *Cocos nucifera*. 11269, 11270. July 21. Identification by S. J. Hughes.

Oidium curtisii (Berk.) Linder

Found twice on rotten wood. 11385, 11400. July 28, 29. Identified by S. J. Hughes.

Additional collections of moldlike fungi were found to be sterile, or when spores were present it was difficult or impossible to determine the method of their production, so that they were unidentifiable.

On the basis of the material seen, both that listed above and that which proved to be unworkable, it would seem that a considerable

[2] Now considered to be synonymous with *S. commune*.

number of fungus species is at work reducing the dead organic matter of the Pacific islands to humus and mineral material. In addition to fungi of these types there are also plant pathogens, soil molds, and probably aquatic fungi on land, and marine fungi parasitizing algae and growing on the ocean floor, especially where there is decaying wood. Recent work in the North Atlantic indicates that there is a population of fungi in marine sediments to considerable depth.

According to the unidentifiable material in Doty's collections, there are several species of polypores, thelephores, and agarics in the mycobiota of Raroia. In addition there are other types of molds associated with wood. In collecting such fungi great care must be exercised in the drying process to insure against the secondary invasion of mold fungi in the tissues and sporiferous areas of the sporophore. It is hoped that additional collections will be made in the Pacific Basin in order that the fungal populations and their activities may become better known.

Notes on Indo-Pacific Scleractinian Corals, Part 3
A New Reef Coral from New Caledonia

JOHN W. WELLS[1]

IN 1957 Dr. R. L. A. Catala of the Station de Biologie Marine, Nouméa, New Caledonia, discovered the brilliant fluorescence in ultraviolet light of the polyps of reef corals living in deeper waters (see, Nature 1(83): 949, 1959; Life 47(3): 64–65, 1959; 26 franc postage stamp of New Caledonia issued March 21, 1958). Dr. Catala kindly sent the writer a collection of these corals, together with photographs of many of them living in the Aquarium de Nouméa. The specimens came from a depth of 35–40 m. on Banc Gail, in the lagoon of Nouméa about 10 mi. from the Aquarium, and were collected by Dr. Yves Merlet, for whom the new species described below is named. The scleractinian fauna includes these species:

Montipora caliculata (Dana)
M. verrucosa (Lam.)
Goniopora lobata Milne Edwards & Haime
Favia speciosa (Dana)
Favites abdita (Ellis & Solander)
Platygyra lamellina (Ehrenberg)
Echinopora hirsutissima M. E. & H.
Trachyphyllia geoffroyi (Audouin)
Galaxea fascicularis (Linn.)
Bantamia merleti sp. nov.
Cynarina lacrymalis (M. E. & H.)[2]
Protolobophyllia japonica Yabe & Sugiyama[2]
Lobophyllia corymbosa (Forskaal)
L. hemprichi (Ehrenb.)
Symphyllia recta (Dana)
Mycedium elephantotus (Pallas)
Euphyllia picteti Bedot[3]
Plerogyra sinuosa (Dana)

[1] Department of Geology, Cornell University, Ithaca, New York. Manuscript received February 1, 1960.

[2] These two species will be the subject of a subsequent note.

[3] Photographs by Dr. Catala of the living coralla of this species show an exact similarity, including color, between its polyps and those of *Pectinia jardinei* Saville-Kent (1893: 39; 1958: pl. 25, fig. 3, and chromo pl. 4, fig. 7) from the northern part of the Great Barrier Reef, and this form probably should be termed *Euphyllia jardinei* (Saville-Kent). *E. picteti* was originally described from Amboina by Bedot and has been reported by the writer (1955: 26) from Port Newry, Queensland.

FAMILY OCULINIDAE

SUBFAMILY GALAXEINAE

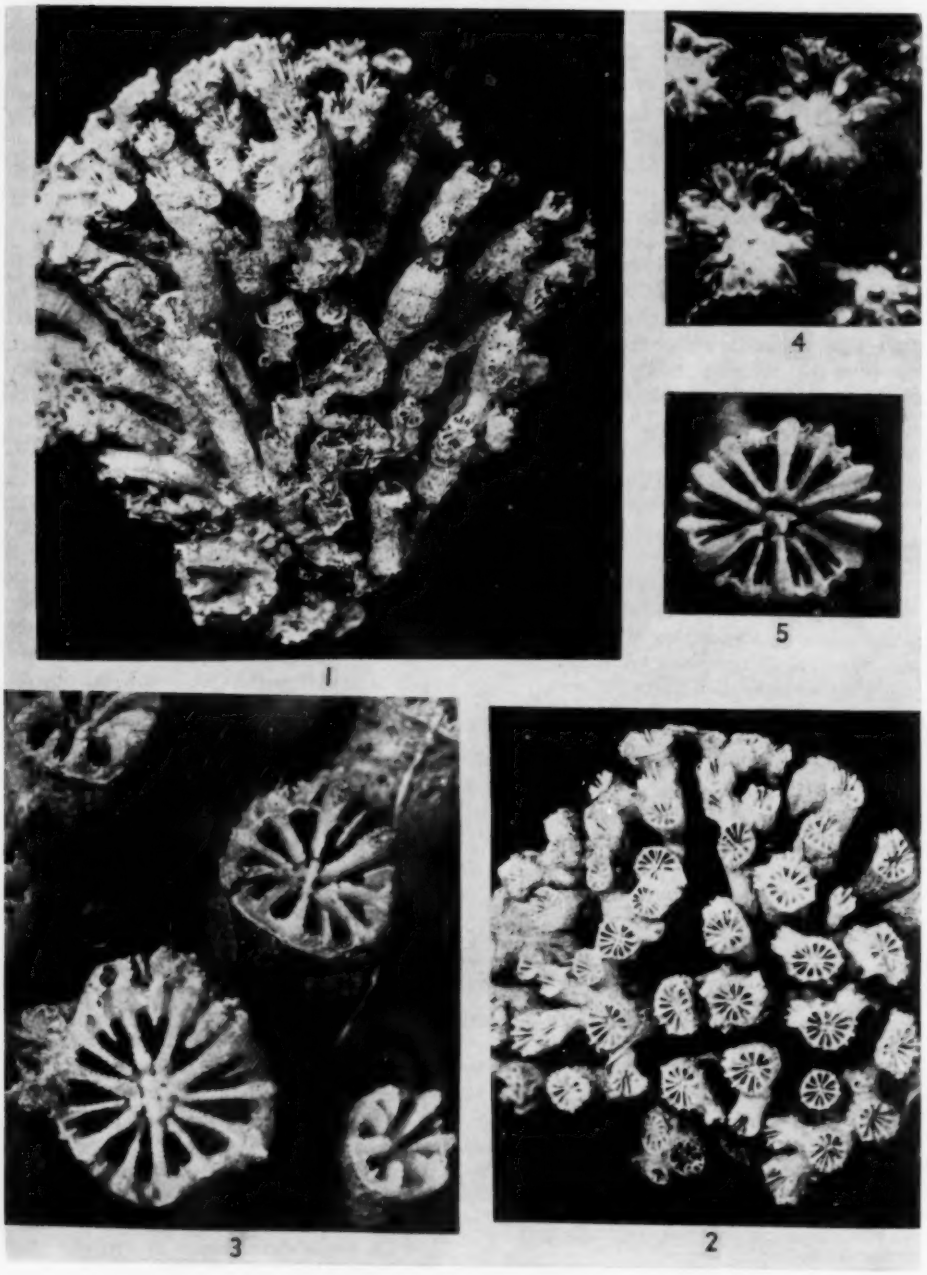
GENUS *Bantamia* Yabe & Eguchi 1943

Bantamia merleti sp. nov.
Figs. 1–4

Corallum fasciculate, 10 cm. in height, 10 cm. broad (holotype), formed by cylindrical corallites, 5–7 mm. in diameter, 4–7 mm. apart, arising by extratentacular budding from a very narrow edge-zone near the calices, at first subhorizontal, then becoming erect and subparallel and losing organic connection with parents. Exterior of corallites costate only near calices, epithecate below, completely lacking any exothecal structures. Calices circular or slightly compressed, 5–7 mm. in diameter, shallow. Septa exsert 1–1.5 mm. near the wall, dropping to low inner lobes near the columella. Septal margins thickened where exsert, nondentate but finely granulated, the granulations extending down septal sides where they are evenly distributed. Septa of first two cycles (12) equal and extending to columella; a few very thin, short septa of the third cycle developed in some systems. Costae weakly developed by narrow edge-zone near calices; in some corallites the edge-zone is not developed and the wall appears epithecal. Columella formed by interlaced loose trabecular processes from inner margins of septa, with one to three granulate papillae arising in bottom of the calice and commonly having a sublamellar aspect. Endotheca consisting of widely spaced, deeply concave single vesicles, the latest ones about 5 mm. below bottom of calice.

Polyps pale brown with pale yellow-green peristomes. Peristomes fluorescing a pale emerald green, the remainder a pale orange-brown.

The reference of this species to *Bantamia* is fairly certain on the basis of Yabe and Eguchi's careful description of the unique specimen of *B. gerthi* from the Miocene deposits of Java. *B. merleti*, also known from a unique specimen, lacks the feeble development of vesicular exo-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theca found in the angles of the branches, has fewer septa in the adult corallites, and has concave rather than tabulate endothecal dissepiments. The range of *Bantamia* thus appears to be extended from the Miocene time to the Recent epoch. *B. merleti* is apparently not a surface reef type but is confined to the deeper lagoon waters.

Yabe and Eguchi considered *Bantamia* to be closely related to *Galaxea*, differing only in the almost complete reduction in *Bantamia* of the extensive vesicular endotheca of *Galaxea* (or the converse?). This skeletal difference implies an almost complete lack of edge-zone in the polyps of *Bantamia*, a distinction confirmed by *B. merleti*. The striking similarity of the calice, septa, and columella of the two genera is emphasized by comparison of the calices of *B. merleti* (Fig. 3) and *G. fascicularis* (Fig. 5). On the other hand, a color photograph by Catala of the living holotype colony of *B. merleti* indicates a considerable difference in the polyps of the two genera. This is not clearly shown in the enlargement (Fig. 4), for the polyps are evidently not fully expanded. According to Fowler (1890: 409) and Matthai (1914: 59), the tentacles of *Galaxea* are ento- and exocoelic, arranged in two rings of 12 each around the prominent (when expanded) oral cone. Saville-Kent (1893: chromo pl. 4, figs. 8–12) and Yonge (1930: 24, fig. 10) show them in a single ring near the edge of the oral disc, the 6 over the first cycle septa standing erect around the oral cone, the 6 of the second cycle and the 12 of the third cycle smaller and normally pointing outwards. The polyps of *Galaxea* are usually partly expanded even in daylight. In *B. merleti* the tentacles total 96, arranged in five alternating rings over the outer half of the oral disc, in the center of which is a small protuberant oral cone. It would appear that the inner three rings, totaling 24 tentacles, are entocoelic, overlying the entocoeles of the mesenterial couples containing the first two cycles and developed parts of the third cycle of septa, in decreasing order of size. The next 24 tentacles, near the periphery, are also entocoelic without corresponding fourth cycle septa. The outer marginal ring of 48 small tentacles is probably exocoelic and extends like a fringe around the edge of the oral disc.

The external morphology of the living reef corals is not yet well enough known to evaluate the taxonomic worth of such differences in tentacular number and arrangement.

Holotype to be deposited in the U. S. National Museum.

Locality: 35–40 m. depth, Banc Gail, Nouméa lagoon, New Caledonia.

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FIGS. 1–4. *Bantamia merleti* n. sp. 1, 2, Lateral and calicular aspects of holotype corallum, ×1; 3, calices, ×4; 4, partially expanded polyps of holotype, ×4 (from color photo by R. Catala).

FIG. 5. Calice of *Galaxea fascicularis* (Linn.), Amboina, ×8 (Bedot, 1907: pl. 11, fig. 44).

Porifera of Friday Harbor and Vicinity

M. W. DE LAUBENFELS[1]

THE PORIFERA of the northwest coast of North America were described rather thoroughly in three papers by L. M. Lambe (1892, 1893, 1894). Many sponges which he treated were from Vancouver Island, near the location herein discussed. Otherwise the Puget Sound Porifera have been little studied.

The present paper is based on a study made by the author during the summer of 1931. Intertidal species were studied living, in the field. Dredged specimens were examined practically immediately upon removal from the water. T. G. Thomson, director of the Oceanographic Laboratories at that time, and other members of the staff, rendered valuable cooperation for which gratitude is hereby expressed.

While other invertebrates were found in considerable variety, amazingly few species of sponges were found to occur in the San Juan Archipelago. The number of individual specimens was large, so that one may conclude that conditions were suitable for the survival and growth of sponges. Notwithstanding careful search of the shores and almost daily dredging for several weeks, the collection consists of representatives of 16 genera, 17 species in all, 2 of which, *Stylissa stipitata* and *Syringella amphispicula*, are new to science. Two species of the class Calcispongiae were found. No dredging was done deep enough to bring up sponges of the class Hyalospongiae. The 15 species of the class Demospongiae represent 14 genera.

CALCISPONGIAE

Leucosolenia nautilia de Laubenfels, 1930

The sponge thus identified was collected July 4, 1931, near the town of Lopez in Lopez Island. It was dredged from a depth of about 60 m.

It consists of a mass of tubes, each somewhat less than 1 mm. in diameter, occasionally anastomosing, but much more frequently branching. The mass of tubes arises from a basal rhizome or reticulation of tubes affixed to the substratum. The maximum distance from this which is reached by the ascending or descending tubes is barely 1 cm. The color in life was white; the consistency softly fragile. The occasional oscules are located at the distal extremities of the ascon tubes and are less than 1 mm. in diameter. The surface is optically smooth, and microscopically somewhat roughened by spicules which protrude, but not at right angles, they lie tangentially in the ectosome, their points directed toward the oscule. Around the oscule in each is found a coronal fringe of special oxeas about 6 $\times$ 300μ. The obliquely placed dermal oxeas are somewhat larger, say about 8 $\times$ 420μ. The principal spicules in among the flagellate cells of the ascon layer are triaxons with rays about 8 $\times$ 140μ. There are a few hypogastral quadriradiates, of approximately the same size as the triradiates.

This is the second record of this species, the first being by de Laubenfels (1930: 25) from Monterey Bay, California. The Puget Sound specimen has somewhat smaller oxeas echinanting the surface than do the California specimens, but otherwise it agrees very closely. The other species of *Leucosolenia* which is probably most closely to be compared here, and which therefore indicates the zoogeographical relationships of the form under discussion, is *Leucosolenia echinata* Kirk (1894: 177) from New Zealand. All its spicules are noticeably larger than those of *nautilia* and it is remarkable that in it the quadriradiates considerably exceed the triradiates in abundance. Furthermore, it is not recorded by Kirk that there were special coronal oxeas, although this may have been the case and they were overlooked by the author.

Scypha raphanus (Schmidt, 1862) de Laubenfels, 1936*a*

The species thus tentatively identified was found growing on the pilings at Friday Harbor.

[1] A posthumous paper, edited by Frank J. Little, Jr., Department of Zoology, University of Texas, Austin, Texas. Manuscript received February 11, 1960.

It is in the form of great pendants tapering at each end, and cylindrical in the central region. Common sizes range from 3 × 30 mm. to 8 × 50 mm. The color in life was dirty white but was considerably obscured by accumulations of foreign material on the surface. The consistency is somewhat elastic but in general very fragile. The surface is minutely hispid, minutely cavernous to the naked eye. The critical difference between this genus (frequently known as *Sycon*) and *Grantia* is in the presence or absence of a special dermis, which is present in *Grantia*.

The structure of the chambers is typically sycon, with elongate thimble shaped chambers frequently as large as 180 × 700μ, but in some portions of the surface shallow and cuplike in shape, in this case being about 130μ in diameter and only 100μ in depth. The oscules are about 2 or 3 mm. in diameter and to the naked eye have smooth rims without conspicuous coronal fringes. Microscopical study shows that coronal spicules are present; they are about 6 × 800μ. The spicules of the chamber layer include smaller oxeas about 5 × 400μ and abundant triaxons with rays 5 × 75μ to 6 × 105μ. Among them occur a very few tetraxons with cladomes of about the same size as the triaxons, but with rhabds considerably shorter. There are raphide-like spicules perhaps to be classified as microscleres. They are only 0.75μ in diameter and so frequently broken because of their delicacy that maximum lengths cannot satisfactorily be assigned.

Lambe (1893: 38) described a *Sycon* (that is to say, a *Scypha*) with specific name *compactum*, from this vicinity. Its dermal oxeas are very much smaller than those of the specimen here described, and the triacts of the chamber layer have shorter rays of the same thickness, but much more sagittal in shape. It possesses a conspicuous subgastral category of triradiates, and in its gastral quadriradiates the rhabds, instead of being shorter than the clads, are longer. Its shape, moreover, is thicker in proportion to the length than is true to the Friday Harbor sponge.

There are two species of *Sycon*, that is to say *Scypha*, described from California. *S. coronatum* was first placed in the genus *Spongia* by Ellis and Solander (1786: 190). It does not have any microxeas. *S. coactum* was described by Urban (1905: 55) as of the genus *Sycandra*. It does have microxeas, but does not have typical tufts to the flagellate chambers, that is to say, spicules projecting from the surface, as is true of the Puget Sound sponge. Furthermore, all the spicules of *coactum* are very much larger than those of *raphana*.

S. raphana was first described by Schmidt (1862: 14) from the Adriatic. There are many minute points of difference between it and the American sponge, but at least *pro tem* this identification may be made.

DEMOSPONGIAE

Haliclona permollis (Bowerbank, 1866) de Laubenfels, 1936*a*

The sponge thus identified was found growing abundantly in a channel at a beach near Argyle on San Juan Island. This was so placed that a strong current rushed past it each time the tide changed. The shape is encrusting with very conspicuous oscular projections. The color in life was a beautiful purple. The consistency is somewhat elastic but rather fragile. The surface, aside from the evident pores, is optically smooth. The oscular projections referred to are about 7 to 9 mm. high, each terminating in a round oscule about 2 mm. in diameter. The total projection, however, is much larger than this, frequently reaching a thickness of 4 or 5 mm. It is very unusual to find such conspicuous oscular tubes on a sponge placed in a strong current, although such are very common in sponges which grow in calm water. The pores are about 100μ in diameter and 200μ or 300μ apart, and as mentioned above, they show very plainly. The internal structure is an isodictyal or "renierid" reticulation of spicules united chiefly at their apices. These are of one sort only, oxeas approximately 7 × 100μ.

This species is clearly conspecific with that which Lambe (1893: 26) recorded from British Columbia and identified as *Reniera cinerea*, a name which unfortunately can no longer be employed, as was shown by de Laubenfels (1936*a*: 39). A lavender species of *Haliclona* of this general type is found in many places in the world. They are separated from each other only by such

items as minute differences in average length of spicule, and it may well be that they are really conspecific, although this is far from certain. From the majority of them the Puget Sound species differs in having considerably shorter spicules. Those of Europe and California, for example, are 140μ long, instead of only 100μ.

Xestospongia vanilla (de Laubenfels, 1930) 1932

The specimen thus identified was found growing intertidally on Brown Island, July 1, 1931. It is a thinly encrusting specimen, at most 2 or 3 mm. thick, and spreading indefinitely laterally. The color is a pale drab, and the consistency is almost stony hard. The surface is smooth and even except for the minute pores and an occasional oscule well under 1 mm. in diameter. The endosomal structure is very dense, the spicules being crowded close together, but permeated by canals which are arranged so frequently at right angles to each other that their pattern is that of a reticulation. The spicules are of one sort only, hastately pointed oxeas about 11 $\times$ 137μ. A few which are much smaller are possibly to be regarded as being not yet fully developed.

This species was originally described by de Laubenfels (1930: 28) as *Haliclona vanilla* and was transferred by him (1932: 116) to the new genus *Xestospongia* with a fairly complete discussion of the species and genus. The Puget Sound specimen is entirely typical, differing in no important respects from the common California species.

Sigmadocia edaphus (de Laubenfels, 1930) 1936*a*
Fig. 2*a*

The sponge so identified was collected on July 3, 1931, being dredged from a depth of 15 m. in Peavine Pass. Large masses aggregating several handfuls, amorphous in shape, were taken at this time. The color in life was pale drab, almost white, and the consistency is stony hard. The surface is comparatively smooth; microscopically it is seen to be abundantly provided with pores only a little more than 100μ in diameter. The oscules average about 10 mm. apart and are nearly 1 mm. in diameter. The interior is rather dense, but is somewhat breadlike in structure, without any conspicuous reticulation of canals. They are united in a somewhat isodictyal fashion, that is to say, connected to each other at their apices in such a way as to make triangular or polygonal meshes. Those immediately at the surface placed horizontally make a network of even finer mesh than that of the endosome. The megascleres of this sponge are of one type only, oxeas approximately 22 $\times$ 285μ. There is also one type of microsclere present, a sigma varying from 40μ to 66μ in length.

The Puget Sound specimen is in very complete agreement with the specimen described as *Gellius edaphus* by de Laubenfels (1930: 28) and discussed by him in more detail and compared to related species (1932: 111). The species was transferred to *Sigmadocia* by de Laubenfels (1936*a*: 69).

Lissodendoryx firma (Lambe, 1894) new transfer
Fig. 1, *A1*, *A2*, *A3*

The sponge thus identified was collected on July 3, 1931. It was dredged from a depth of 75 m. near Turn Island.

It is a compactly massive sponge, only 4 or 5 cm. in greatest diameter and in life was a rich orange color. The consistency is firm, somewhat elastic. The surface is slightly tuberculate, but in general might be described as smooth, a very evident special dermal reticulation being fine grained. The pores are minute and the oscules are represented only dubiously by a few openings much less than 1 mm. in diameter which possibly were mere accidental ruptures in the surface. The interior is dense, provided with only a small amount of open space in the form of canals or gross chambers. The special dermal tornotes are hastately pointed tylostrogyles 7 $\times$ 343μ. The principal skeleton is made up of a more or less confused dense mass of smooth styles, exceptionally large for this genus. They are 36 $\times$ 440μ. The microscleres include arcuate isochelas of one sort, length 43μ, and sigmas of one sort, length 30 to 32μ.

This species was first described as *Myxilla firma* by Lambe (1894: 122). It may appropriately be compared to *Lissodendoryx kyma* de Laubenfels, 1930 (p. 27). This California sponge lacks the sigmas, and all of its spicules are notably smaller than those of *firma*. It should be commented, however, that *kyma* and *firma* are remarkable in the genus for the exceptionally

large size of the spicules; they are doubtless related forms.

Lissodendoryx noxiosa de Laubenfels, 1930
Fig. 1, *B1*

The specimen thus identified was dredged on July 3, 1931, at a depth of 15 m., in Peavine Pass; masses aggregating several handfuls came up in the dredge.

The shape is amorphous and the color in life a dull yellowish drab. The characteristic unpleasant odor was very much in evidence in life, and seemed to be identical with the odor of the California specimens to the best of the recollection of the author. The consistency is softly spongy, fragile. The surface is irregularly tuberculate, but otherwise is optically smooth because the dermal skeleton is of very fine mesh. Rather numerous oscules are scattered about, averaging somewhat under 1 cm. apart, and 0.5 to 1.5 mm. in diameter.

The endosome is very much like the structure of a crumb of bread, the spicules being arranged primarily in bunches, but otherwise in a somewhat isodictyal reticulation in the masses surrounding the numerous gross chambers. The special dermal spicules may be described in general as being tylotes, but very frequently there is a rounded promulgation at each end, as though they were strongyles with a tylote enlargement near but not at each end. Others of them have one end larger than the other and the smaller end somewhat spined. The variety of shapes is quite remarkable. The endosomal spicules are smooth styles, with here and there what may be interpreted as an incipient spine. Only arcuate chelas 28μ were in evidence as microscleres.

This species was described by de Laubenfels (1930: 27) from California, where it is very abundant, and yet it is doubtful if any California specimen has attained the very large size of the Puget Sound one. Lambe (1894: 121) had a *Lissodendoryx* which he identified as *Myxilla barentsi* Vosmaer, 1885 (p. 27). This was almost certainly the form at present under discussion and not the arctic species of Vosmaer. Lambe's specimen had as its principal spicules styles with small spines on them. Whereas this is not common, it is really the case in the Peavine Pass specimen and various California specimens also show this tendency. Lambe's specimen had sigmas, as do the California specimens. The latter variety has megascleres about thirty percent shorter but not thinner than those of the Puget Sound sponges. Taken by itself alone, this is a trivial difference. The general agreement, and especially the very distinctive odor render it possible to make the identification with *noxiosa* very confidently.

Burtonanchora lacunosa (Lambe, 1892) de Laubenfels, 1936*a*

The sponge thus identified was dredged on July 3, 1931, in Peavine Pass, at a depth of 15 m. It is a small subovate mass about 2 × 3 cm. The color in life was fleshy pink, and the consistency is softly spongy to fragile. The surface, otherwise smooth, is rendered irregular by the pore areas and oscules mentioned below. There is definite evidence of the presence of a special dermal layer. The round oscules are nearly 1 mm. in diameter and are scattered here and there more than 1 cm. apart in most places, but occasionally as little as 2 mm. apart. Except within regions about 2 or 3 mm. from the oscules, the entire surface of the sponge is dotted with pore areas each nearly 1 mm. in diameter and about 2 mm. apart, center to center. Each of these circular areas is a sieve with the pores approximately 100μ in diameter, and crowded closely together.

The endosomal structure is between subisodictyal and confused. The special dermal spicules are inequi-ended hastately pointed tornotes, about 7 × 220μ. The endosomal spicules are somewhat spiny styles 12 × 220μ. The microscleres include sigmas 23μ long, and isochelas slightly longer. The latter are here interpreted as being anchorate, but they are far from being typical anchorate chelas, verging strongly towards the arcuate.

Lambe (1892: 70) described a sponge from the vicinity of Vancouver as *Myxilla lacunosa*, which is rather clearly the form under discussion but which has one difference, i. e., that the principal spicules according to Lambe were not spiny. At the same time (p. 71) Lambe records another *Myxilla* which he identifies as being *rosacea* of Lieberkühn (1859: 521). This second specimen has the principal spicules like the Pea-

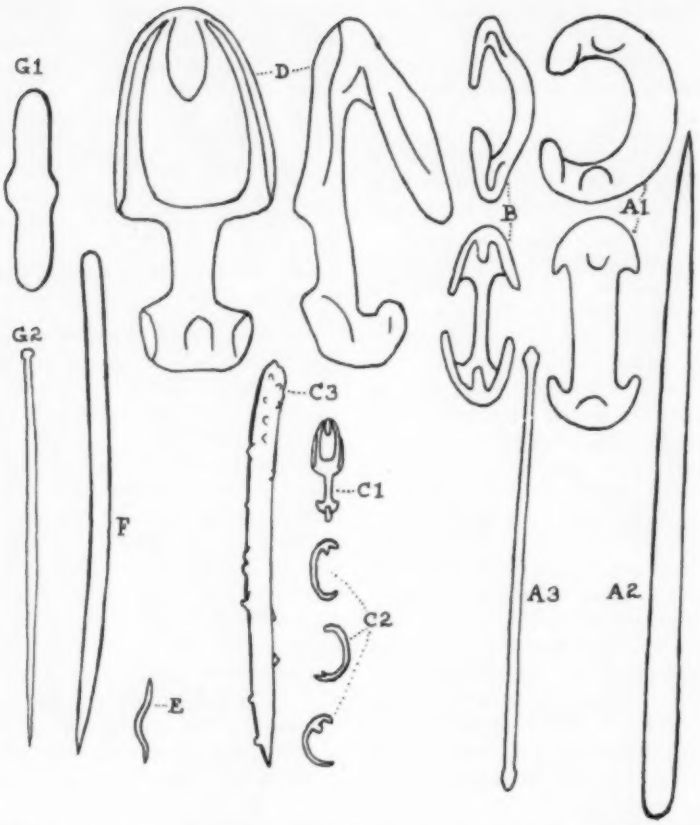

FIG. 1. *A, Lissodendoryx firma* (Lambe): *1,* chelas, × 880; *2,* style, × 212; *3,* dermal tornote, × 212. *B, Lissodendoryx noxiosa* de Laubenfels; chelas, × 880. *C, Iophon chelifer* var. *californiana* de Laubenfels: *1,* anisochela, × 212; *2,* bipocilli, × 212; *3,* acanthostyle, × 212. *D, Mycale adhaerens* (Lambe); anisochela, × 880. *E, Ophlitaspongia pennata* (Lambe); toxa, × 212. *F, Stylissa stipitata* new species; style, × 212. *G, Choanites suberea* var. *lata* (Lambe): *1, microstrongyle,* × 880; *2,* tylostyle, × 212. (All from camera lucida drawings.)

vine Pass specimen now being discussed. Its isochelas and sigmas were both, however, about double the length of those of his *lacunosa* and those of the Puget Sound sponge. It is very frequently the case in the Myxillinae that there are two categories of chelas, a larger and a smaller, and two categories of sigmas, a larger and a smaller. One or the other of these may be common while the other is rare. It may be that there exists in the vicinity of Puget Sound but a single species, properly to be termed *lacunosa*, having a full complement that includes larger and smaller chelas, and larger and smaller sigmas. It may be that in a specimen which Lambe described as *lacunosa* he found only the smaller microscleres, and in the one he identified as *rosacea* he found only the larger. It is here proposed that the specimen identified by Lambe as being *rosacea* should be dropped in synonymy to his *lacunosa*. Neither of these two specimens described by the latter author possesses the peculiar arrangement of the surface found in the

sponge from Peavine Pass, but Lambe (1894: 121) described from the vicinity of Alaska a sponge which he named *Myxilla behringensis*. The dermal spicules and microscleres are very like those of his *lacunosa*, and significantly the endosomal spicules vary from entirely smooth as in his *lacunosa* to spiny as in the specimen he identified as *rosacea*. This *behringensis* did have the peculiar arrangement of the pores and oscules of the specimens herein described. It seems probable that only one species is involved in all of these descriptions, and it is therefore proposed that *Myxilla behringensis* Lambe be dropped in synonymy to his *lacunosa*, which was transferred to the genus *Burtonanchora* by de Laubenfels (1936*a*: 94).

Ectyodoryx parasitica (Lambe, 1893) de Laubenfels, 1936*a*

This species is exceedingly abundant in the vicinity of Friday Harbor, occurring apparently always on the shells of bivalve mollusks belonging to the genus *Pecten*. In fact, practically every specimen of *Pecten* collected in this vicinity seems to have been utilized by the sponges. Usually the sponges are of this species, but occasionally *Mycale adhaerens*, to be described below, is also found on the shells. Two hundred and two such sponge-covered pectens were taken for study, and of them 183, or well over 90 per cent, proved to have *Ectyodoryx*. Nineteen had the *Mycale*. It was further noticed that in each case when both the valves of the pelecypod were abundantly covered with sponge, that the mollusk was always a male, though not all males were so distinguished.

The crust has a relatively smooth surface, although showing many openings such as pores and oscules. Thickness may attain to 12 or 15 mm., and lateral extent is of course limited by the size of the shell. The color in life is a dull grayish drab and the consistency is weakly spongy or fragile. The surface is abundantly covered with rather coarse pores and oscules about 1 mm. in diameter, irregularly scattered.

The endosome is "crumb-of-bread" in appearance and consistency. The special dermal spicules are hastately pointed tornotes, verging slightly upon the tylote shape. They are from 4 $\times$ 130μ to 6 $\times$ 145μ. The endosomal or principal spicules are styles, usually acanthose, about 11μ in diameter, but ranging in length from 190 to 270μ. Occasionally the spines are almost or completely wanting, which is very interesting in comparison to the preceding species, as is also the fact that there are two categories of isochelas present. These are anchorate, the larger being 54μ in length, while the smaller are only 14μ in length. There are also two sizes or categories of sigmas, each respectively about the size of the corresponding isochelas.

This species was originally described by Lambe (1893: 31) from Vancouver Island, as *Myxilla parasitica*. It was reviewed by de Laubenfels (1936*a*: 84) and its correct location in the genus *Ectyodoryx* was shown by him.

Tedania fragilis Lambe, 1894

The specimen thus identified was dredged northeast of Blakeley at a depth of between 50 and 66 m., on July 6, 1931. It is an encrustation less than 1 cm. thick, and about 2 $\times$ 4 cm. in area. In life it was flesh colored, and the consistency is very soft, fragile and compressible. The surface is comparatively smooth, almost glabrous. Pores and oscules can not be made out.

The endosome is rather dense to the unaided eye and microscopically is seen to be packed with plumose tracts, which is an axinellid characteristic usually not so pronounced in the genus *Tedania*. The special dermal tornotes are hastately pointed, 4 $\times$ 200μ. As may be expected the principal skeleton consists of styles, 3 $\times$ 150μ to 7 $\times$ 400μ, but it is most astonishing to note that some of these are more or less covered with small spines. The microscleres are onychaetes as is absolutely typical for the genus *Tedania*; these are long thin rhaphides 1 $\times$ 150μ to 3 $\times$ 200μ which are covered by characteristic roughenings, rather than pronounced spines.

A specimen which must surely have been conspecific with the one under discussion was described as *Tedania fragilis* by Lambe (1894: 116). It was a more typical *Tedania*, not possessing the unusual shape of the styles. Identification of the Puget Sound sponge with *Tedania* is rather confidently made, however, because of the very characteristic microscleres.

Iophon chelifer californiana de Laubenfels, 1932
Fig. 1, *C1, C2, C3*

The sponge so identified was dredged northeast of Blakeley on July 6, 1931, at a depth of between 50 and 66 m. It is an amorphous mass about 2 × 3 × 5 cm. In life it was a dull drab color, gradually turning black in alcohol. This is characteristic of the genus *Iophon*, and is exhibited by few, if any, other genera in quite the same way, i. e., some turn black suddenly upon exposure to air, etc. The consistency is softly fragile, crumbling. The surface is irregularly tuberculate, with a smooth dermal membrane much in evidence. This is broken off in many places, leaving numerous internal cavities exposed. It is difficult to say whether any oscules show or not; there are what appear to be oscules, but these may be merely places where the dermal membrane has been broken off, exposing the underlying cavities.

The interior is "crumb-of-bread" with an isodictyal reticulation of masses of spicules placed around minute cavities. The special dermal spicules are tylotes 4 to 7μ in diameter and 280μ long. The principal spicules are acanthostyles, reaching a maximum size of 16 × 320μ. The microscleres include palmate isochelas of the peculiar shape characteristic of the genus, and also bipocilli 13μ long, which resemble tridentate unguiferate anisochelas.

Ridley and Dendy (1886: 349) described *Iophon chelifer* and Lambe (1893: 30) recorded a sponge from the vicinity of Vancouver as of this species. There are differences from the typical race which were pointed out by de Laubenfels (1932: 82) in connection with specimens which he had from California, for which he established the subspecies *californiana*. The Puget Sound specimens correspond very closely with those from California, and one need have little hesitation in regarding them as of the same variety. It is very probable that the specimens described by de Laubenfels (1928: 361), as *Burtonella melanokhemia* are also conspecific with this variety of *chelifer*.

Ophlitaspongia pennata (Lambe, 1894) de Laubenfels, 1927
Fig 1, *E1*

This species was found growing on Brown Island, just across from the laboratory of the University of Washington. It is an exceedingly thin crust as found at Puget Sound, only 1 or 2 mm. thick, and spreading indefinitely laterally. The color at the time of collection was dull brown. The consistency is somewhat compressible, rather like that of soft wood. The surface is irregular with notable grooves radiating around minute oscules, only 200μ or 300μ in diameter.

The structure consists of innumerable little plumose columns extending up perpendicularly from the base and little if any connected to each other except by protoplasmic structures. The bulk of the spicules in these tracts are subtylostyles 16 to 20μ in diameter and about 330μ long. Near the surface many are found which are only 3 × 200μ; these may or may not constitute a separate category. Toxas about 40μ long are occasionally found among the smaller spicules near the surface.

This species was described as *Desmacella pennata* by Lambe (1894: 129). It is an exceedingly abundant sponge along the Pacific Coast of the United States, extending far down in California, almost to the Mexican boundary. It is noteworthy for its ability to survive intertidal conditions, often growing nearer the high tide mark than is true of other species of sponge. The species was transferred to the genus *Ophlitaspongia* by de Laubenfels (1927: 265). For a further discussion of the species, reference may be made to his paper on the sponges of California (1932: 103).

Mycale adhaerens (Lambe, 1893) de Laubenfels, 1936*a*
Fig. 1, *D1*, 2 B

This species occurs abundantly in the vicinity of Friday Harbor upon bivalve mollusks of the genus *Pecten*. As noted above in connection with *Ectyodoryx parasitica*, about 10 percent (or slightly less) of the *Pectens* in this vicinity have *Mycale* as the sponge which covers the shell.

The color in life is a dull grayish drab, and the consistency is softly spongy to fragile. The surface is nearly smooth, and what openings are found are susceptible to interpretation as being accidental ruptures in the dermis rather than structural oscules.

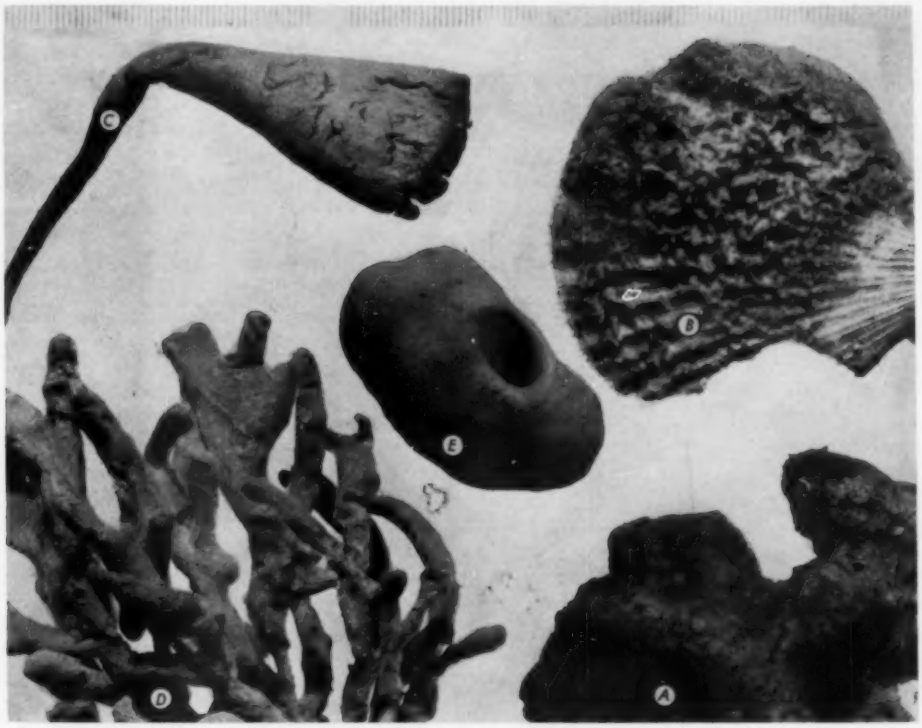

FIG. 2. *A, Sigmadocia edaphus* de Laubenfels. *B, Mycale adhaerens* (Lambe). *C, Stylissa stipitata* new species. *E, Choanites suberea* var. *lata* (Lambe).

The structure of the interior is very fibrous, the fibers themselves being plumose as seen under the miscroscope. They probably contain a small amount of spongin, but are composed chiefly of abundant rows of spicules, which are smooth styles, reaching a maximum size of about 10 × 320μ. However many are as small as 8 × 300μ and the smaller spicules occasionally show a tendency to be tylostylote. There are very numerous stout palmate anisochelas of three size ranges, 14 to 15μ, 27 to 28μ and 56 to 60μ. This largest category frequently has the spicules associated together in symmetrical groupings known as rosettes. There are also two size ranges of sigmas, the smaller having a chord length of about 20μ, and the larger of 35μ.

This sponge may be readily distinguished in the field from the other *Pecten*-covering sponge, *Ectyodoryx parasitica*, by the very fibrous structure of the interior of the *Mycale*, and the greater ease with which its ectosome may be detached from the endosome.

This species was originally described as *Esperella adhaerens* by Lambe (1893: 27) and the genus was later shown to be synonymous with *Mycale* by de Laubenfels (1936*a*: 122).

Stylissa stipitata new species
Fig. 1, *F1*, 2 C

The holotype, USNM no. 22687, was collected near False Bay of San Juan Island. It was dredged at a depth of 20 m., only 100 m. off

shore. Other specimens were taken later in the same month, July, 1931, at a depth of 45 m. at Griffin Bay.

This species is typically funnel-shaped with an elongate stem. The maximum diameter of the cone is at the distal end and at that place is 20 mm. across. The thickness of the wall is only 2 or 3 mm., and at the thinnest the stem is also only 2 or 3 mm. in diameter. The total length, or height, of the sponge is approximately 10 cm., of which 5 or 6 cm. may be described as stem, the remainder being the hollow funnel, shaped like an inverted cone.

The color in life was light drab. The consistency is spongy, very flexible, tough, and not easily torn.

The surface is moderately smooth to the naked eye, especially on the exterior of the sponge, where there is an obvious ectosomal specialization of very fine meshed reticulation. This is frequently cracked, but other than this, no oscules are evident. It is probable that the efferent openings are the abundant minute ones on the interior of the hollow funnel.

The spicules on the interior are arranged in a rather confused manner, but in general with the points towards the surface. The adjective "plumose" might be applied to the appearance in many places. There can be little doubt that this is axinellid structure. The megascleres show typical axinellid variation in size. Only smooth styles have been found; these are $2 \times 180\mu$ to $4 \times 366\mu$.

The genus *Stylissa* was established by Hallman (1914: 349) to have as genotype the sponge described as *Stylotella flabelliformis* by Hentschel (1912: 355). This East Indian species is very much like the Puget Sound one here described, except that its spicules are somewhat larger, and it is cup-shaped without any stem. Another similar sponge is that for which Gray (1867: 513) established the genus *Tragosia*, a species originally described as *Spongia infundibuliformis* by Linné (1858: 1348). It is very like the one under consideration except that it is shorter of stem and is usually broader and more cup-shaped. It is tremendously more hispid as to the surface, and its spicules include oxeas as well as styles. It is typically an European species.

Syringella amphispicula new species
Fig. 2 D

The holotype, USNM no. 22707, was dredged July 24, 1931 at a depth of 45 m. in Griffin Bay. It is a ramose sponge, with a very few anastomoses between the gnarled and misshapen branches. The latter are 3 to 10 mm. thick and about 6 cm. high, with obtuse, club-shaped ends. The color in life was ochre yellow, the consistency very tough and flexible. The surface is even but undulating, nearly lipostomous.

There is a dense axial specialization of longitudinally arranged megascleres, among which spongin may have been present, but not conspicuous. This axis often has a diameter slightly more than half that of the entire branch. In the flesh around this axial core the spicules are arranged perpendicular to the surface and at right angles to the axis. The spicules are exclusively tylostyles, many about $18 \times 670\mu$, but also much smaller. Numerous very small ones (say $2 \times 100\mu$) may be immature forms, or may constitute a separate category, but are connected to the larger type by numerous intermediates. The different sizes are mixed among each other, not localized.

This new species is unique in the genus *Syringella* for its abundance of the smaller spicules, that in it nearly make up a second size range. Many (but by no means all) of the species of this genus have a central hollow to the branches. Many have more spongin than does *amphispicula*.

Cliona celata Grant, 1826

The sponge thus identified was dredged from a depth of about 5 or 10 m. on July 3, 1931, south of Turn Island. It was found growing in a mass of broken barnacle shells, making subcircular tunnels 0.5–1.5 mm. in diameter. From them minute papilles protrude here and there a distance of about 1 mm. in life. The color in life was lemon yellow. The consistency is soft and the spicules are arranged in a rather confused fashion within the tunnels. The spicules are of one sort only; tylostyles about $10 \times 285\mu$.

This sponge was originally described by Grant (1826: 79) from Europe, but it is a well-

known cosmopolitan sponge. Its wide distribution may be due to the fact that it bores in the shells of mollusks which may transport it freely from place to place. It frequently disintegrates the shells completely in the course of time, and may do serious damage to commercial oyster beds. As an older sponge it grows up and out from its earlier boring habitat to make large yellow masses, frequently the size of a man's head. Such were not found in Puget Sound, however; only a few small boring specimens being recorded.

Choanites suberea var. *lata* (Lambe, 1892) de Laubenfels, 1936*a*
Fig. 1, *G1–2*, 2 E

The sponge thus identified is moderately common in the vicinity of Friday Harbor, frequently occurring on hermit crab shells, which may in the course of time be completely replaced by the sponge so that no trace of the calcareous material remains, except that the sponge preserved the shell-shape as a mold might.

The total mass is frequently more than 3 cm. in diameter. The color in life was gray white and the consistency was stiff, cartilaginous or cork-like. The surface is optically very smooth; pores are not in evidence, but a few oscules 2 to 4 mm. in diameter are found, usually from only one to three per sponge.

Within the sponge the spicules are densely packed, although there are distinctive gross canals 0.5 to 1.5 mm. in diameter. An even denser ectosomal region which might almost be described as a cortex extends from 0.3 to 0.7 mm. below the surface. In it practically all the spicules are placed with their points toward the surface, whereas this is frequently but not always the case in the interior of the sponge. These ectosomal spicules are perhaps slightly smaller than those of the endosome. The megascleres of this species are of one sort only, tylostyles 5 × 280 to 6 × 180μ. The microscleres are centrotylote microstrongyles 24μ long.

This species was described from European specimens as *Spongia suberea* by Montagu (1818: 100). The Puget Sound species in question was first described by Lambe (1892: 71) as *Suberites latus*. This was recorded from California by de Laubenfels (1932: 52) where it is reduced to a subspecies of *Ficulina suberea*. The genus *Ficulina* being a complete synonym of *Choanites*, however (de Laubenfels 1936*a*: 144), the genus must be designated according to the prior appellation. The principal or European variety has slightly smaller spicules, and is frequently, though not always, rosy red in color.

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Studies of the Biology of *Polychoerus carmelensis* (Turbellaria: Acoela)

KENNETH B. ARMITAGE[1]

LITTLE IS KNOWN about the biology of the Acoela. Hyman has summarized both earlier (1951) and more recent studies (1959: 731 and f.). The Acoela are of particular interest because typically they lack a gut and lack protonephridia, and frequently lack eyes. Thus they carry on a number of biological activities without having the structural modifications associated with these activities. The biology of the Acoela is of further interest because of the hypothesis of Hadzi that the Acoela are the stem group of the Eumetazoa and were derived from ciliates (de Beer, 1954; Hanson, 1958).

Polychoerus carmelensis is found in the pools of the mid-tide horizon in the vicinity of Monterey, California (Ricketts and Calvin, 1952: 49). Costello and Costello have described copulation (1938*a*) and egg laying (1939) in this species.

These studies were conducted at the Hopkins Marine Station of Stanford University, Pacific Grove, California, where the author was studying marine biology as a National Science Foundation science-faculty fellow. I wish to express my appreciation to Dr. L. R. Blinks, director of the Hopkins Marine Station, for providing facilities, and to Dr. Donald P. Abbott for introducing me to *P. carmelensis*.

REACTIONS TO SALINITY

Animals were collected from the tide pools during low tide at Point Pinos and Carmel Point. They were returned to the laboratory and placed in a flat, rectangular glass dish through which sea water (s.w.) flowed. Solutions of 25, 50, 75, 100, 125, and 150 per cent s.w. were made. The dilute solutions were made by mixing sea water from the laboratory pipes with the appropriate amount of distilled water. The concentrated solutions were made by evaporating sea water to form a 200 per cent solution and then diluting this with appropriate amounts of distilled water.

The first experiment was to determine the range of tolerance to salinity. Twenty animals were placed in each of the dilutions of s.w. They were observed for activity every hour during the first 12 hr. and then were checked every 12 hr. for 5 days. Any animals surviving after 5 days were periodically checked for another 2 weeks after which time the experiments were discontinued. Two tests were made for activity. The dishes were shaken gently; healthy animals reacted to this agitation by showing some movement in place or by locomotion. A bright light caused normal animals to locomote. Animals that did not respond to either stimulus were considered inactive until disintegration of epidermal cells was evident, at which time the animals were considered dead.

25 per cent s.w. All animals curled into a U-shaped position immediately upon being placed in the dish. After 1 hr. all animals were dead. The individuals showed a marked swelling and disintegration of the epidermal cells.

50 per cent s.w. Most animals curled into the U-shaped position within 10 min. After 1 hr., only abnormal body movements, characterized by twisting and contractions, were evident. The worms would not attach to the dish, and several extruded material, including copepods that had been engulfed, from the mouth. After 5 hr. 10 animals were transferred to normal sea water. Two hr. later half the worms were active. After 3 hr., 7 of them were active and the other 3 were uncurled. By the end of 16 hr. all animals displayed normal activity. Seven of this group were active 2 weeks later when the experiment ceased.

At 54 hr. 5 of the remaining 10 worms in 50 per cent s.w. were disintegrating and the other 5 showed some slight muscular movement when stimulated. The 5 active worms were transferred to normal s.w., but none of them survived.

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75, 100, 125 per cent s.w. All animals in these concentrations showed normal activity for 2 weeks. After 16 days, 3 animals in 125 per cent s.w. died.

150 per cent s.w. Most animals curled up shortly after being placed in the dish. One hr. later, 3 responded to the light stimulus and 7 responded upon being touched with a glass rod. The low level of activity was maintained without detectable change for the next 14 hr. By the 15th through the 24th hr. movement was limited to 4 worms who could expand and contract their anterior ends, but could not move their posterior ends. Most animals were in the U-shaped position, but some curled into an oval position. At 42 hr. a few showed feeble movements, 4 were disintegrating, and the remainder were in the U-shaped position. Twenty-four hr. later all of the animals except 3 were disintegrating and only 1 was capable of any movement.

The second experiment was set up to determine if the worms are capable of acclimating to levels of salinity. The experiment was not designed to determine the range of acclimation to salinity, but to demonstrate that acclimation was possible. Fifty animals were placed in 75 per cent s.w. 96 hr. prior to testing. Survival times in 30, 40, 50, 60, and 70 per cent s.w. were determined for worms acclimated to 75 per cent s.w. and 100 per cent s.w. Ten animals were placed in each solution.

30 per cent s.w. All worms were immobile. In 2 hr., 7 of the group acclimated to 100 per cent s.w. and 3 acclimated to 75 per cent s.w. were sloughing epidermal cells. At 8 hr., all of both groups were disintegrating.

40 per cent s.w. All animals of both groups were immobile and failed to respond to normal stimuli. However, at 8 hr. 7 of the group acclimated to 75 per cent s.w. responded to a light stimulus from a no. 2 photoflood. Six of these were still active at 12 hr. and 5 showed feeble movements at 24 hr. None of the group acclimated to 100 per cent s.w. showed any response at any time.

50, 60, 70 per cent s.w. The number of animals surviving in each of these three concentrations is plotted against time in Figure 1. The curves for the animals tested in 50 per cent s.w.

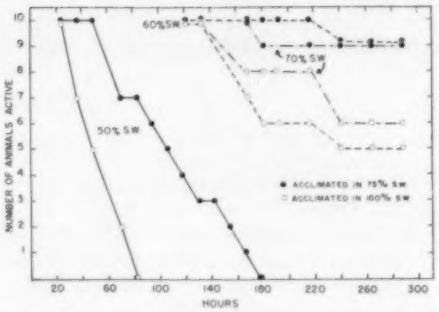

FIG. 1. Number of active animals plotted against time for *P. carmelensis* acclimated to 75 per cent s.w. and 100 per cent s.w. and tested in 50, 60, and 70 per cent s.w.

indicate that acclimation has taken place and has acted to increase survival time in the acclimated animals. The curve also indicates that the difference in survival time between the two acclimated groups increases with increasing time in the test environment. The curves also illustrate the variability in tolerance to salinity among individuals. This is particularly evident in the curves for the animals tested in 60 per cent s.w. and in 70 per cent s.w. After the least tolerant individuals of the worms acclimated to 100 per cent s.w. died, all the groups reached an equilibrium with essentially all the remaining animals surviving.

DIURNAL RHYTHM

The only known case of a persistent rhythm in the phylum Platyhelminthes has been reported for the acoel *Convoluta roscoffensis* (Harker, 1958). The worm comes to the surface of the sand at low tide and disappears into the sand when the tide returns. The rhythmic behavior is maintained in the laboratory for about 1 week in vessels of still water and is independent of day or night. *P. carmelensis* is found on the upper surfaces of algae or gravel during low tide and disappears into the gravel as the tide returns. The similarity between the two species makes desirable a study to determine if a diurnal or tidal rhythm occurs in *P. carmelensis*.

About 150 worms were collected near Pt. Pinos and brought into the laboratory. Ten animals along with a few pieces of rock were

placed in each of 10 plastic bowls. Two additional bowls were filled with gravel and 10 worms were placed in each. All the bowls were placed in an aquarium with the sides and top covered to keep out all light. In addition, the room was also darkened. Sea water from the laboratory system was circulated around the plastic bowls as a temperature control. The number of animals visible in each bowl was determined approximately every 2 hr. from 0800 until 2200 hr. for 2 days and spot-checked for 2 more days. The counts were made under a dim light.

During the first day there was a gradual increase in the number of worms that were visible. This leveled off by the morning of the 2nd day. The number of animals visible at the time of each count for the 2nd day is given in Table 1. There is no relationship between the number of animals visible and the time of day or the condition of the tide. Nor did the subsequent spot checks indicate any relationship. From this it is concluded that *P. carmelensis* does not show any diurnal or tidal rhythm of activity.

Observations in the field indicated that *P. carmelensis* came to the surface during low tide when the water was quiescent in the tide pools and when the light was relatively dim. If one waded through a pool in which the animals were located, one could observe the animals begin a downward movement. A similar downward movement was observed when the first waves of the incoming tide reached the pool. These observations indicated that water agitation was the stimulus for movement downward.

The following laboratory experiment tested the field observation. The data in Table 1 show that there was not much variation in the number of animals visible in the plastic bowls in the darkened aquarium. The number observed was particularly stable in the plastic bowls with gravel. Two bowls with rocks and two bowls with gravel were lighted sufficiently so that the animals could be counted. There was no reaction to the light in any of the dishes. Each of the bowls with gravel had 10 animals visible. One bowl was shaken gently; all the animals immediately became active and began crawling down into the gravel. After 3 min., only 2 worms were visible and both of them were crawling. All 10 animals remained visible in the control dish which was not shaken and only 1 animal was active. There were 5 worms on top of a rock in a third bowl. When this bowl was agitated, all the worms became active; 4 of them crawled under the rock within 2 min. The other animals in the bowl also became active, but could not move down as they were on the bottom of the dish. There was no activity in the fourth bowl, which also had a rock and served as an unshaken control to compare with the third bowl. From these experiments and from the field observations, it was concluded that *P. carmelensis* is negatively geotaxic in quiet water and positively geotaxic in agitated water.

TABLE 1

TOTAL NUMBER OF ANIMALS VISIBLE IN PLASTIC BOWLS WITH ROCK AND WITH GRAVEL
(Ten animals were placed in each bowl)

TIME OF OBSERVATION	NO. VISIBLE IN 8 BOWLS WITH ROCK	NO. VISIBLE IN 2 BOWLS WITH GRAVEL	TIME OF TIDE
0800	56	19	
			0810 low
1000	64	20	
1200	62	20	
1400	48	19	
			1444 high
1500	54	19	
1600	62	20	
2000	51	20	
			2105 low
2200	53	17	

During low tides when bright sunlight was present, *Polychoerus* was found under rocks and gravel, indicating that the genus might be positively geotaxic under bright light.

Twenty-one animals were distributed in six 25 × 75 mm. plastic vials so that there were at least 3 worms in each vial. The worms were allowed to come to rest after being added to the vials. The number of worms on the side of the vials was determined. Then the worms were stimulated for 3 min. with various intensities of light. All activity was recorded. The worms were kept in total darkness for 1 hr. between subsequent tests. The same worms were used throughout. The results are summarized in Table 2. Low light intensities had essentially no effect on the animals. Higher light intensities resulted in an increase in over-all activity with all animals becoming active at the highest intensity of light. Animals never crawled upward. There was an increasing percentage of animals on the sides of the vials that crawled downward with the increase in light. This experiment indicates that *P. carmelensis* becomes more active with increasing light intensity, and where directed movement is possible the animal crawls away from the source of light. Thus the absence of animals on the upper surface of rock and gravel during low tide and bright sunlight can be attributed to the reaction to light demonstrated above.

REACTIONS TO LIGHT

In the previous section some of the reactions of *P. carmelensis* to light were described. That experiment was designed to explain part of the upward and downward movement of the worms in the intertidal substrate in the absence of a diurnal rhythm. The reactions to light led to some further exploration of the behavior of the worms in relation to light.

The increase in the number of animals showing locomotion on the bottom of the vials at higher intensities of light (Table 2) indicated a photokinetic response. Photokinesis is usually defined as a change in the rate of undirected locomotion resulting from a change in the intensity of light. The photokinetic response in *P. carmelensis* was measured in two experiments.

The first experiment was designed to measure the rate of crawling under varied intensities of light. Two narrow strips of plastic were fastened 6 mm. apart in the bottom of a petri dish with a diameter of 14 cm. The plastic strips and the bottom of the dish were covered with black friction tape. A 5 cm. course was marked off between the plastic strips. The course was illuminated from one end. A worm was dropped into the dish at one end of the course with the light turned on, and the time that elapsed until the worm reached the end of the course was determined. The behavior of the worms was highly erratic. Some of them spent considerable time in turning the head from side to side, others ceased crawling before reaching the end of the course, and some crawled directly down the course. All of the worms were photonegative at the intensities used. Because of the variability in behavior, the experiment was discontinued after a small series of determinations were made. The rates of crawling for worms that crawled directly down the course illuminated by means of 5 ft. c. and 37 ft. c. were analysed by means of an analysis of variance and the between groups variance was statistically significant. The mean rate of travel was 0.86 mm/sec at 5 ft. c. and 1.34 mm/sec at 37 ft. c. The rate of crawling increased about 55 per cent when the light intensity was increased about 640 per cent. Similar slight increases in the rate of crawling with large increases in the intensity of light were found for *Dugesia gonocephala* and *Plagiostomum* sp. (Carthy, 1958: 37).

A second experiment attempted to measure photokinesis by determining the amount of activity initiated in a population of quiescent worms illuminated at various intensities of light. Five worms were placed in each of five petri dishes filled with sea water. After 1 hr., the worms were illuminated dorsally at various light intensities for 3 min. The time in seconds for a worm to respond was determined, as well as the nature of the response. Responses were of three types, (1) head raising; (2) body movement in which the animal might swing the anterior end side to side several times or show other changes in body form, but remaining essentially in the same location in the dish; (3) locomotion, in which the animal actively crawled about the dish. An activity index was determined

TABLE 2

REACTIONS OF *P. carmelensis* TO LIGHT OF VARIOUS INTENSITIES
(A total of 21 animals in 6 vials were tested for 3 min. at each intensity)

LIGHT INTENSITY ft. c.	NO. ON SIDES	NO. MOVING DOWN	PER CENT MOVING DOWN	HEAD MOVEMENT AT SURFACE	LOCOMOTION ON BOTTOM
1.7	15			1	
10.0	9			1	
37.0	8			3	2
130.0	11	4	36	3	5
225	8	7	87	1	12
400	5	5	100		16

by assigning an arbitrary value of 5, 10, and 20, respectively, to each of the above responses and dividing the sum of the values for individual worms by the sum of the number of seconds that elapsed until the animal responded or until 180 sec. elapsed. Animals that did not respond were included. This may be illustrated in the following equation:

$$\text{Activity index} = \frac{\text{sum of arbitrary values of response for all worms}}{\text{sum of number of sec. until response or until elapse of 180 sec. for all worms}}$$

The activity index will be higher if the number of animals responding to the stimulus increases or if the nature of the response is of a higher level or if both of these occur. The results are presented in Figure 2. Activity appears to be linearly related to light intensity over the ranges of light intensity studied. It is difficult to know if this relationship is a real one, for it might be an artifact of the method used to determine activity. However, the raw data indicate such a linear relationship, so that this relationship seems reasonably accurate. It probably does not exist at higher intensities, for once an animal has responded fully it can no longer respond to an increased stimulus.

On contrasting backgrounds, planarians come to rest on the darker ground (Ullyott, 1936). This reaction was tested in *P. carmelensis* in the following manner. Half the bottom, the sides, and the upper edge of the sides of a 4½-in. petri dish were painted black and the other half of the bottom was painted white. The dish was half-filled with sea water and placed in a metal trough through which sea water circulated to maintain a relatively constant temperature and illuminated from above by 15 ft. c. of light. Ten (in some experiments, 20) animals were added to the petri dish as close to the center as possible. The animals were allowed 1 hr. to come to rest, after which the animals on each background were counted. The dish was rotated 90° between trials so that if the animals were reacting to light being reflected from the wall of the room or from the sides of the dish, such a directional orientation could be detected. The position of rest of each animal for each trial was plotted on a drawing of a petri dish. There was no evidence of directional orientation in any of the experiments. Forty different individuals were used in the first set of experiments. All animals were kept in the dark between trials. Any animal that crawled up on the side of the dish was considered to be on a black background. The experiments extended over 5 days. Of 40 animals tested, 33 came to rest on the white background and 7 came to rest on the black background. The marked orientation to the white background (chi square = 16.8, $p < 0.001$) was unexpected in view of the results with planarians. The testing was repeated four times using the same animals. The results were similar in all cases. Since all of the animals came from an area of broken shell, most of which was white, it was postulated that the animals were acclimated to the white background. If this hypothesis were correct, then it should be possible to acclimate the worms to a black back-

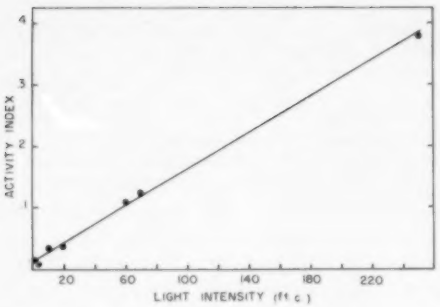

FIG. 2. The activity index of a population of *P. carmelensis* plotted against light intensity. Curve fitted by eye.

ground. Twenty animals were kept under constant light in a black plastic bowl for 96 hr. The animals were tested at 24, 72, and 96 hr. At 24 hr., 12 animals oriented to white and 8 to black, showing no significant difference (chi square $= .8$, $p < 0.5$), 72 hours, 8 oriented to white and 12 to black, again showing no significant difference. At 96 hr., 5 oriented to white and 15 to black, now showing a significant difference (chi square $= 5.0$, $p < 0.05$). The animals were tested again 2 days later. During the two days, they were kept on the black background but received light only from 0800 to 1800 hr. Several tests were run, with the animals being kept in darkness between tests. In the first test, 5 animals stopped on the white background and 15 on the black background. The marked orientation to the black background was significant (chi square $= 5.0$, $p < 0.05$). However, when the test was repeated using the same animals, two of the tests gave essentially the same results, but the third showed no difference in background selection.

A second series of tests for background choice was made with newly collected worms from Carmel Point. Forty worms were placed in black dishes and 40 were placed in white dishes. The worms were kept under constant light and tested after 96 hr. The testing extended over 2 days and the animals were kept in darkness during the period of testing. The animals were tested under 35 ft. c. of light. The animals kept on a white background went to the white side of the dish 27 times and to the black side 11 times. The selection of the white background is highly significant (chi square $= 6.7$, $p = c. 0.01$). The animals kept on the black background went to the white side of the dish 9 times and to the black side 29 times. The selection of the black background is highly significant (chi square $= 10.5$, $p < 0.01$). Each of these tests was repeated once using the same animals. Results were essentially identical.

The animals were kept in their respective dishes and given 48 hr. of constant light. They were then placed in the dark and subsequently tested under 70 ft. c. of light.

The animals kept on a white background went to the white side of the dish 21 times and to the black side 16 times. There is no indication that background selection occurred (chi square $= 0.66$, $p < 0.5$). However, the animals kept on a black background went to the black side of the dish 33 times and to the white side 7 times. Selection of the black background was significant (chi square $= 16.0$, $p < 0.001$). Each of these tests was repeated twice using the same animals. The worms acclimated to the black background showed about the same pattern, but with lowered chi-square values. The animals acclimated to the white background showed almost complete randomness in selection of background (chi square $= 0.01$).

These is no ready explanation for the shift in background selection by the worms acclimated to the white background. The experiments concerning photokinesis demonstrated that the worms had a differential sensitivity to light, some reacting to a weak stimulus, others to a strong stimulus. Because of the variation in sensitivity to light, it seems reasonable to postulate that under the increased light intensity, photokinesis was stimulated more in the light-sensitive animals. These sensitive animals then oriented to the black background to reduce the amount of stimulation. The less sensitive animals continued to orient to the white background to which they were acclimated. That there is a threshold of sensitivity to light whereby the reaction to light stimulation is reversed is indirectly indicated. Costello and Costello (1938*b*) reported that *P. carmelensis* may "... be positively phototropic to moderate light intensities"; the positive phototropism was

evidenced by the gathering of the worms on the lighted side of the aquarium in which they were kept. Taxic reactions were not studied as such in this series of experiments, but the experiments on diurnal rhythm demonstrated that the animals were negatively phototaxic at high light intensities and showed no response at low intensities. Thus the possibility of a differential response to low and high light intensities exists, as has been found for other animals (Clarke, 1930; Baylor and Smith, 1957). Clarke (1932) found that a change of illumination must rise above a certain threshold to be effective in causing a reversal of phototropic signs in *Daphnia*.

It was mentioned previously that worms acclimated to a black background showed a lesser degree of choice of the black background when the tests were repeated. Since the animals were kept in darkness except while being tested, it seemed possible that some of the worms were losing their acclimated condition and perhaps were moving in a more random manner. Therefore, both the animals acclimated to a white background and the animals acclimated to a black background were illuminated with 70 ft. c. for 12 hr., placed in darkness for 12 hr., and then tested. Thirty of the animals acclimated to the black background came to rest on the black background while 8 selected the white background. The orientation to the black background was highly significant (chi square $= 12.6$, $p < 0.001$). Nineteen of the animals acclimated to the white background came to rest on the white background and 19 selected the black background. Thus it was not possible to condition the animals to select the white background under 70 ft. c. of light under the conditions of the experiment. However, the animals acclimated to the black background responded almost to the same degree as in the original test. This experiment suggests that failure to maintain an orientation to a white background at 70 ft. c. is a result of animals more sensitive to light changing their orientation from the white background to the black background.

FEEDING BEHAVIOR

Five *P. carmelensis* were placed in a Syracuse watch glass with a dozen copepods, *Tigriopus californicus*. One of the copepods came to rest near the left anterior end of a *Polychoerus* which had stopped crawling. The anterior end of the worm was raised and with a sudden whiplike movement it was brought down over the *Tigriopus*. The worm assumed a cup-shaped position over the copepod. The copepod was quickly engulfed and its movements inside the body of the worm could be observed. These movements continued for 10 min. The capture of the crustacean by *Polychoerus* was similar to the manner of prey capture by the acoel *Convoluta paradoxa* (Jennings, 1957). Dead *Tigriopus* were not ingested.

CONCLUSIONS

1. *P. carmelensis* can tolerate salinity conditions ranging from 75 to 125 per cent s.w. indefinitely. Worms were quickly inactivated at concentrations of sea water above and below these values. Animals kept in 50 per cent s.w. for 5 hr. and transferred to 100 per cent s.w. recovered normal activity by 16 hr. after transfer.

2. *P. carmelensis* was acclimated to 75 per cent s.w. and survival time was increased at the range of salinities tested over controls acclimated to 100 per cent s.w.

3. There was no evidence of a diurnal or tidal rhythm of activity. Worms tended to be negatively geotaxic in quiet water at low light intensities and positively geotaxic in agitated water or at high light intensities.

4. Photokinesis, measured as the amount of activity in a population of worms, was linearly related to light intensity over the range of light intensities used. Only slight differences were found in the rate of crawling of worms over a measured course under highly different intensities of light.

5. At 15 ft. c. light intensity, worms collected from tide pools with white shell and rock chose the white background when placed in a petri dish with half the bottom painted white and the other half black. Worms were acclimated for 96 hr. in dishes painted black and in dishes painted white. The black-acclimated worms chose the black background and the white-acclimated worms chose the white background when tested in the petri dish with contrasting backgrounds of black and white. The reaction was

highly significant at 15 ft. c. and 30 ft. c. However, at 70 ft. c., the worms acclimated to a white background showed no preference when tested on contrasting backgrounds. The worms acclimated to the black background continued to orient to the black background when tested on contrasting backgrounds. It was postulated that the change in response at 70 ft. c. of animals acclimated to the white background was a result of crossing a threshold of light sensitivity so that the more sensitive animals tended to orient to the black background while the less sensitive animals tended to orient to the white background.

6. The capture of a copepod prey is described.

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Preliminary Tests of the Toxin Extracted from California Sea Hares of the Genus *Aplysia*[1]

LINDSAY R. WINKLER[2]

DURING A STUDY of the biology of California sea hares (Winkler, 1957), the large amounts of absorbed but unused substances from the sea hare's diet which are to be found in the digestive gland were noted. On the assumption that if there are toxic sea weeds in the diet of the sea hare these toxins might possibly be present in the digestive gland, samples of the exudate from frozen digestive glands on hand were removed with a small pipette and were placed in test tubes. The test tubes were then placed in a boiling water bath for 10 min. After being centrifuged, milliliter aliquots were injected intraperitoneally into 20-gm. C57 black mice. The digestive glands of *Helix aspersa* O. F. Muller were similarly treated as controls. The animals injected with the experimental extract showed almost immediate respiratory symptoms followed by an excitement stage and death in 4 to 6 min. Since neither the controls nor ashed samples reconstituted and injected produced these effects, further study seemed desirable. Certain general aspects of the resulting study are reported here.

It may or may not be significant that Latin and Medieval writers, beginning with Pliny (*ca.* A.D. 60) considered the sea hare to be very poisonous and claimed its use in poisonings during the days of Imperial Rome. An excellent summary of the beliefs and superstitions pertaining to the sea hare is given by Johnston (1850).

MATERIALS AND METHODS

Collections in March, April, and May were made at Doheney Beach near Dana Point, California. Later collections were made from May through August at Lunada Bay, Palos Verdes, Los Angeles County, California. The former were small specimens between 4 and 6 in., the latter were large breeding specimens measuring to 1 ft. in length. Animals were collected at low tides, packed in wet *Pelvetia fastigiata*, and transported back to the laboratory where they were either immediately dissected or were refrigerated until the next day. In either case, the animals were alive when dissected and no difference in the toxic effect was noted between those dissected immediately and those stored overnight.

The digestive glands were dissected out by making a longitudinal, midpedal cut with scissors in the ventral surface of the foot from the tail to the lip area. The animal was then turned inside out. The digestive gland was removed, including the part of the intestine embedded in the gland and the ovotestis, which is an integral part of the digestive gland complex. The percentage weight of the digestive gland complex to the weight of the intact animals was determined in a certain number of cases. Samples of the crop and/or intestinal contents were preserved in alcohol and studied where it seemed desirable in a rough attempt to ascertain if the diet was responsible for the toxicity. Specimens of *Aplysia vaccaria* Winkler were also collected and dissected for extraction. The digestive glands were stored in glass containers in a deep-freeze and were not thawed until ready for use.

It early became apparent that a more refined method of extraction than the water methods used initially was necessary because of the large amounts of pigments, salts, and apolar materials present in the gland. After much trial and error the following method proved the most satisfactory for large-scale crude extract preparation. Thawed digestive gland (130–150 gm.) is placed in a Waring Blendor. When the gland is thoroughly liquified, 400 ml. of acetone is

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slowly added, and after a few minutes the entire mixture is quickly filtered. The residue is then rinsed with an additional 100 ml. of acetone. The acetone extract, containing the tissue "water" from the digestive gland is then placed in the flask of a rotary evaporator, partial vacuum being supplied by an aspirator. As the percentage of acetone is reduced by evaporation, the apolar fraction is thrown out of solution and deposited on the flask wall. When the remaining "water" has been evaporated to about 50 cc., it is placed in a refrigerator overnight, after which it is refiltered and becomes what is referred to as the crude extract.

The routine bio-assay procedure for indicating relative strength of extracts in the toxic principle consists of injecting 1 ml. of an extract intraperitoneally into mice of similar weight and observing the death time to the last heartbeat audible with a stethoscope. The death time serves as a rough indication of the relative toxicity.

Initial LD_{50} values were obtained by conventional methods using three groups of mice to establish three points on a graph plotting percentage mortality against dose given. The LD_{50} values were then read from the graph. Subsequent LD_{50} approximations and those for the chick were determined using a minimum number of animals by the "up and down" method proposed by Dixon (1959). Since the LD_{1-99} range is very narrow, this latter method gave adequate results for the present purposes.

EXPERIMENTAL RESULTS

The average percentage weight of the digestive gland/ovotestis complex of *A. californica* based on 15 specimens was 10.8 per cent, and the range was from 8.4 to 14.0 per cent. Varying amounts of sand were found in the intestines of this species, which influenced the accuracy of the weights. The accuracy was higher for *A. vaccaria*, however, since no sand was found in the intestines. The average percentage based on 5 specimens of the latter species was 19.4 per cent, ranging from 18.0 to 20.3 per cent.

The diet varied between the two collecting sites. At Doheney Beach the diet followed the predominant flora consisting of several coralline algae and *Hypnea californica*. A considerably wider variety of seaweeds was noted in the Lunada Bay collections. The Lunada Bay sea hares appeared to be more toxic but this may have been the result of more maturity or merely a reflection of variation in the extraction efficiency. No correlation is possible at the present state of the research.

Aplysia vaccaria, a sea hare rather distantly related within the genus, possesses a similar toxin in its digestive gland.

The LD_{50} was determined for 23-gm. mice and is expressed in grams of digestive gland tissue. Two different batches of raw material were used to obtain two somewhat removed values. Each batch represents the material obtained from 5 to 12 sea hares, depending on the animals' size. One batch collected May 4, 1959, had an LD_{50} value of 0.65 gm. tissue for a 23-gm. mouse (0.028 gm/gm body weight). Another collected at the same location July 28, 1959, had a value of 0.8 gm. per 23-gm. mouse (0.036 gm/gm weight). However, the difference in the two values may represent only differences in extraction efficiency rather than true variation in toxin concentration.

The LD_{50} for 3-day-old baby chicks was found to be only slightly less than 25 per cent more than that for mice.

When mice are injected intraperitoneally with the crude toxin of somewhat more than the LD_{50} dosage, there is an almost instantaneous hyperventilation. Ears are drooped and the mouse usually sticks his nose in a corner of the cage and salivates profusely. After a varying time in which hyperventilation is evident, the mouse starts scurrying about the cage, usually leaving a trail of urine. Perhaps it then returns to its corner or begins to demonstrate occasional muscular twitching which may turn into uncontrolled attempts at movement suggesting a convulsion. This uncontrolled movement may develop in waves and once begun is always terminal. Ataxia and inability to right itself usually develop before or during these uncontrolled movements. The animal passes into a completely relaxed state. The heart continues for some time at a reduced pace, gradually becoming weaker until it can no longer be heard with a stethoscope. The toxin also killed mice

when given by stomach tube at approximately 12 times the intraperitoneal LD_{50} dose.

Helix aspersa O. F. Muller withstood doses of the toxin sufficient to kill several mice with only temporary effects. However, the purple shore crab quickly went into a relaxed state when small quantities were injected at the podial interstices. Since they were presumed dead, they were not observed further.

When frogs are injected with the LD_{50} dose/gm weight for mice, the dorsal appendages become weakened and paralyzed in approximately 5 min. This is followed quickly by relaxation (Fig. 1), complete except for the anterior limbs, which become spastic. The rectus abdominis is also tensed. The muscles controlling the eyes are the last to become paralyzed. A complete deathlike stupor follows, lasting about 15 hr. The first reaction to reappear is the movement of the nictitating membrane and retraction of the eyes. Soon thereafter, when teased in the eye region, an isolated leg twitch may occur, usually in the thigh region. As time progresses, teasing produces an initial kick followed by complete immotility for a time. In 3 to 5 hr. more the frogs recover completely.

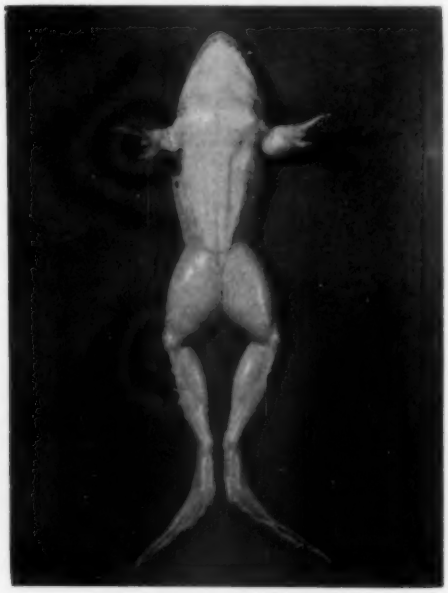

FIG. 1. The reaction of the frog to the toxin of *A. californica*. Note the tensed abdominal muscles and forelegs.

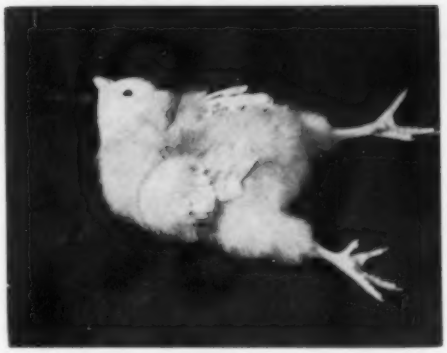

FIG. 2. The reaction of the chick to the toxin of *A. californica*. The toxin was injected subcutaneously over the breast.

Three-day-old baby chicks were injected with lethal doses to observe symptoms. Immediate hyperventilation occurred, followed in order by ataxia, relaxation of the wings, and a stretching of the legs (Fig. 2), which were relaxed only terminally. Hypersalivation and difficulty in swallowing were apparent. Respiratory arrest preceded a final convulsive effort before complete cessation of movement.

Rats and guinea pigs show symptoms quite similar to those of the mouse. Kittens, on the other hand, passed through a short but violent wretching and vomiting stage. Hyperventilation, relaxation of the vocal cords and nictitating membrane, and dilation of the pupils followed. Relaxation of forepaws and neck muscles preceded respiratory distress, violent tail wagging, terminal respiratory arrest, and relaxation of the bladder sphincter muscles.

DISCUSSION AND CONCLUSIONS

The common denominator of the lethal symptoms observed seems to be respiratory paralysis with no other noticeable lethal effects. Frogs, though able to survive doses paralyzing their lung respiration for 15 hr. or more, succumbed sporadically to a wide range of much larger doses. This may indicate other less dominant

lethal effects masked by the respiratory arrest. However, respiratory arrest seems to be the limiting factor in birds and mammals, though a suggestion of other contributing effects is noted in the chick. Studies on isolated preparations are now in progress and will be reported later.

At the present stage of the study it is impossible to postulate the function, if any, or the ultimate source of the toxin. The absence of any method for the animal to inject the toxin along with the high dosages required to be effective orally would seem to preclude any defensive use. However, both concentration of the toxin from the seaweed diet or an endocrine function may be considered as possibilities.

SUMMARY

1. The digestive gland of *Aplysia californica* and *A. vaccaria* contain a water- and acetone-soluble toxin.

2. Crude extracts produced muscular weakness and death by respiratory arrest when injected intraperitoneally into various laboratory animals or given orally at about 12 times the IP dose.

3. Frogs survived a respiratory arrest and complete paralysis for 15 hr. When extracts are given in much larger doses, death ensues from causes not yet determined.

4. From observation of these symptoms, it is suggested that the primary lethal effect in mammals and birds is respiratory arrest, though other less dominant lethal effects seem to operate in the frog.

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A Contribution to the Biology of the Convict Surgeonfish of the Hawaiian Islands, *Acanthurus triostegus sandvicensis*[1]

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THE SURGEONFISHES (family Acanthuridae), which are distinctive chiefly in their possession of a knifelike spine or spines at the base of the tail, are one of the dominant groups of tropical inshore marine fishes. Over much of their vast range, including Hawaii, where they are especially prominent on the reefs, they are important components of subsistence fisheries. Little is known of their biology, however. There are only scattered references to the herbivorous food habits of the group and general remarks on the habitat of certain species.

An analysis of the generic classification of the family and taxonomic revisions of some of the genera have been published (Randall, 1955 *a*, *c*, *d*; 1956*b*). The largest genus, *Acanthurus*, contains 32 species, 4 of which occur in the Atlantic, and the rest in the Indo-Pacific. The present paper constitutes a report of a study made during 1952–55 upon the life history and the ecology of one Hawaiian subspecies of this genus, *A. triostegus sandvicensis*, the convict tang or convict surgeonfish. In Hawaii and elsewhere in Polynesia this surgeonfish is known as the manini, and hereafter it will usually be referred to by that name.

The manini is the most abundant species of surgeonfish in the Hawaiian Islands and commercially the most important. Judging from its prevalence in museum collections, it is also common elsewhere in the Indo-Pacific region. Jordan and Seale (1906: 354) wrote, "This species is the most abundant of the genus about Samoa, swarming everywhere on the reefs." The young reside in tidepools, and are therefore more accessible for observation and experimentation than the young of other acanthurids in Hawaii which are usually found in deeper water. The species has the widest distribution of all of the surgeonfishes—East Africa to the Gulf of California (a single record from West Africa by Fowler, 1936, should be confirmed). Thus interest in its biology may be greater than that of a localized species.

A. triostegus (Fig. 1) has been described under 10 different scientific names and placed in six different genera. Nomenclatural considerations and description of the species and variants, with special reference to fin-ray counts and coloration, have been dealt with previously (Randall, 1956*b*).

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H. W. Manter and Leland S. Olsen of the University of Nebraska, Paul Illg of the University of Washington, Cadet Hand of the University of California, J. Percy Moore of the University of Pennsylvania, and Alan Lewis of the University of Hawaii, assisted in the identification of parasites.

Most of the photographs were taken by Charles E. Cutress of the U. S. National Museum.

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FIG. 1. Adult manini, *Acanthurus triostegus sandvicensis*, from Hawaii. Standard length, 154 mm.

HABITAT

In the Hawaiian Islands the manini occupies a diversity of habitats. It occurs in bays, harbors, and exposed reef areas. It abounds in tide pools and shallow water, yet is known at depths of at least 100 ft. Areas of very turbid and brackish water are usually avoided, but a few manini have been collected even in these regions.

Like most reef fishes, the manini avoids extensive stretches of sand or mud bottom, preferring instead the nearness of holes or crevices in the reef for shelter and solid bottom for the growth of its algal food.

The manini appears to be more restricted in habitat in the Gilbert and Marshall islands, possibly because of the sharper definition of the ecological zones of these atolls. It occurs in these atolls both in the lagoon and outer reef areas; however it seems to be confined to relatively shallow water. On the outer reef the fish were seen only on the reef flat, the young in great abundance in the shallower sections and the adults on the seaward portions (for data from a reef-flat transect in the Gilbert Islands, see Randall, 1955*b*: 181). The species was only rarely observed in the turbulent surge channel zone and was never seen on the coralliferous terrace (benched area of living coral offshore from the reef flat).

As in the Gilberts and Marshalls, the presence of heavy coralline areas in the Hawaiian Islands seems to limit the manini. This is apparent from the underwater transect work of Brock (1954). Areas like the northern part of Kealakekua Bay, Hawaii, where the coral growth is extremely rich for the Hawaiian region, are almost devoid of manini. Since this species is herbivorous, its diminution in coral areas may be associated with the small amount of substratum available for the growth of algae. Surprisingly, other surgeonfishes such as *Acanthurus leucopareius*, *A. achilles*, *Zebrasoma flavescens*, and *Ctenochaetus strigosus*, usually less abundant than manini, are the most common fishes in this part of the bay. With the exception of *C. strigosus* which is a detritus feeder (Randall, 1955*d*), these species are more inclined to crop close to the substratum than the manini, judging from the greater amount of inorganic debris in their stomach contents, and they may therefore be superior competitors under such conditions.

The eggs and larvae of the manini are pelagic. This has been ascertained by a study of development following artificial fertilization of the eggs, by the capture of larvae in plankton nets, and by the taking of the late postlarval or acronurus stage at night lights offshore.

A total of 11 acanthurid larvae (at least 3 of which are manini), 4.2–8.7 mm. in total length, were found in the plankton collections from Hawaiian waters of Cruises 4 (May 1950) and 6 (August 1950) of the "Hugh M. Smith," a POFI research vessel. These fish were taken at eight stations ranging from about 10 to 140 mi. from the nearest island (for more exact locations, see King and Hida, 1954: fig. 1, stations 1A, 10, 13, 15, 17, and 23 of Cruise 4 and stations 7 and 14 of Cruise 6). They were captured in horizontal tows made with fine-meshed plankton nets (1 m.) which sampled three different levels simultaneously. For both cruises combined, a total of 58 hauls were made at the surface, 24 at a depth of 50 m., and 112 at depths from 100 to 300 m. Six of the larvae were taken at the surface, 5 at 50 m., and none at greater depths. The failure to find more larvae in these collections is probably due to the distance from land of most of the stations. Only 6 of the 29 stations of each cruise were within 25 mi. of any of the Hawaiian Islands and only 1 within 10 mi. The absence of larval *Acanthurus* longer than 8.7 mm. in the collections is probably due to the ability of larger larvae to elude

the plankton net. The lack of specimens shorter than 4.2 mm. may be the result of a paucity of small larvae so far offshore.

That acanthurid larvae, in general, are more abundant close to land has been shown by Reintjes and King (1953). These authors found a total of 1,067 acanthurid larvae in the stomach of 184 of 1,097 yellowfin tuna (*Thunnus macropterus*) sampled from the region of the Line and Phoenix islands. They stated that the acanthurids were common in the stomachs of nearshore yellowfin, along with balistids and carangids. Representatives of the Bramidae, Exocoetidae, and Gempylidae predominated in the stomachs of offshore yellowfin.

King kindly allowed me to examine the stomach content work sheets in order to compare the occurrence of larval acanthurids in the stomachs of tuna caught at the surface by pole-and-line fishing and by trolling with those caught at depths of about 30 to 160 mi. by long-lining. The comparison revealed more acanthurid larvae in the stomachs of surface-caught fish.

The acronurus larval form of the manini, averaging about 26 mm. in standard length in the Hawaiian Islands, leaves the pelagic realm and enters very shallow water, often tide pools, to transform to the juvenile stage. Although juveniles tend to remain in shallow water, there is a progressive movement with increasing size to somewhat deeper water. Adults are not entirely absent from tide pools, however. Several were seen in pools 1–3 ft. deep cut off from the open sea at low tide on Moku Manu and Manana (Rabbit) islands. Also, at night on Oahu, manini as large as 70 mm. were occasionally found in high tide pools.

TOLERANCE TO TEMPERATURE AND SALINITY

In order to determine if the manini is capable of surviving the extremes of temperatures and salinity which it encounters on Oahu, a survey of these factors in tide pools and brackish areas known to be penetrated by the species was undertaken and compared with the tolerance of the species to these factors as determined by laboratory experiments on both juveniles and adults.

Environmental Extremes

The survey of environmental temperature and salinity was not made on any regular schedule. Only when conditions occurred which suggested that high and low values of temperature and salinity might be found, were measurements of these factors made. Temperatures were taken at mid-depth of the tide pools tested. Water samples from which chlorinity was determined were obtained after stirring the pools. The Mohr method was used to determine chlorinity, and the results are expressed as grams of chlorine per kilogram of sea water (‰).

The maximum temperature, 35.1° C., was recorded in a tide pool with basalt bottom (almost black) at Makapuu Point on August 31, 1953, at 2:00 P.M. A reverse stratification of temperature existed in the pool at that time. A +0.2 low tide had occurred at 1:50 P.M. The maximum air temperature at Makapuu Point for August 31 was 79° F. (26.2° C.). Other fishes observed in the tide pool along with manini included aholehole (*Kuhlia sandvicensis*) and kupipi (*Abudefduf sordidus*).

The minimum temperature, 16.2° C., was recorded in a small tide pool at Diamond Head on March 5, 1954, at 11:15 P.M. A –0.2 low tide had occurred at Honolulu at 10:42 P.M. The minimum air temperature during the night was 60° F. (15.5° C.). A strong northerly wind was blowing. The wind velocity for the hour prior to the temperature reading was as high as 33 knots.

The extremes of environmental temperature recorded by Tester and Takata (1953: 48) for the aholehole on Oahu are 20.1° C. and 32.1° C. Like the manini, young aholehole are tide-pool residents. Although found in the highest pools of the intertidal zone, they are less inclined than the manini to enter small pools. A more notable difference of these two species is the ability of the aholehole to live in streams with little or no salt content.

The lowest chlorinity recorded from pools where manini were observed was 2.65 ‰. This reading was obtained from a high tide pool at Diamond Head during a heavy rain at 9:00 A.M. on March 1, 1954. A +0.1 low tide occurred at 9:02 A.M. A rivulet of rain water was observed entering the pool.

Another low chlorinity (3.62 ‰) was obtained in a sample taken from the shore of the Ala Wai Canal at the Ala Moana Bridge on February 23, 1954, following a heavy rain. Although manini could not be seen at the time because of the turbidity of the water, they were observed in the area prior to the rain and after the water had cleared.

The highest chlorinity was 21.30 ‰. The water sample was taken from the pool at Makapuu Point in which the 35.1° C. temperature was recorded.

Experiments on Temperature Tolerance

The experiments on temperature tolerance were performed on manini which were maintained in aquaria at a near-constant temperature of 24° C. for at least 24 hr. The fish were placed singly in a gallon jar of sea water at the temperature of the aquarium from which they were taken. The jar was then lowered into a water-filled copper compartment containing either a heating unit or a refrigerating unit and brought to the test temperature in 1 hr. ± 10 min. The fish were kept at this temperature for 1 hr. If death ensued before the end of this hour, the time was recorded. The duration of the test period was chosen as a rough approximation of the temporal conditions of exposure to temperature extremes experienced by manini in high tide pools. Throughout the tests the jar was strongly aerated.

At about 5° C. before the maximum or minimum temperatures were reached, the fish began to increase their rate of swimming and darted around the jar. As the lethal temperature was approached more closely, the equilibrium of the fish was affected. They swam on one side, upside down, or in small circles. The last major activity was usually a rapid, spasmodic, swimming movement, often in a short spiral.

The results, except those of tests of both juveniles and adults run at temperatures of 36.5° C. or less and 13° C. or greater (which caused no deaths), are shown in Table 1.

Although the data are not adequate to determine individual variation in the region of the temperature extremes, it seems evident that a range of about 13° to 36° C. is withstood by this species in the Hawaiian Islands, disregarding the possible extension of this range by acclimatization.

TABLE 1

TEMPERATURE TOLERANCE OF *Acanthurus triostegus sandvicensis*

STANDARD LENGTH (mm.)	TEST TEMP. (° C.)	MINUTES TEST TEMP. ENDURED
96	37.0	45
97	37.0	60
137	37.5	25
96	37.6	10
86	38.0	4
97	38.0	15
101	38.2	6
103	38.3	20
26	36.8	40
27	37.2	60
28	37.5	60
34	37.6	15
29	37.8	60
28	38.0	60
29	38.0	18
28	38.1	2
103	13.3	60
95	12.2	60
140	10.1	10
122	9.0	2
25	13.6	2
27	12.8	10
27	12.5	60
28	11.6	5
27	11.0	60
32	10.8	8

Although the range of temperature which manini can withstand appears to be extralimital to the extremes normally encountered by the species in the Hawaiian Islands, information supplied by D. W. Strasburg in a letter suggests that juvenile manini in the southern Marshall Islands are, upon occasions, killed in tide pools by heat. On August 17, 1950, a high tide pool, about 30 sq. ft. in surface area and 1 ft. deep, on the ocean side of Arno Atoll was observed at low tide to contain two small *Acanthurus triostegus triostegus* and one small *Istiblennius edentulus*. Several hours later the two manini were dead. The blenny was still living. The temperature of the pool at mid-depth was 41° C.

Experiments on Salinity Tolerance

Salinity tolerance experiments on manini were carried out in a 30 gal. aquarium. All fish were retained in aquaria at least 24 hr. before use in experiments. The fish were not exposed to the test salinity suddenly. Instead the salinity was gradually changed over a period of 2 hr. either by the removal of aquarium water and replacement with tap water (previously allowed to stand for at least 12 hr.) or the addition of salt from evaporated sea water. Fish were held at the test salinity for a maximum of 24 hr. The long period of exposure to salinity extremes was chosen because manini entering brackish areas may be subjected to water of low salt content for at least this length of time.

The results are given in Table 2. Omitted are trials run at chlorinity values greater than 1.4‰, none of which caused any deaths. No trials were run at chlorinities greater than 38.25 ‰.

Although more data are needed to determine with accuracy the minimum salinity which manini can withstand, it seems evident that manini in tide pools can tolerate a greater range in salinity than they normally experience. Since they cannot live in water of extremely low salinity, they probably do not enter fresh-water habitats.

PREDATORS

Predation on the manini is probably most acute during the early stages of the life history, but I have no information on the identity of the many pelagic animals that must feed on the eggs and small larvae. The large number of post-larval stages of acanthurids found in the stomachs of adult yellowfin tuna has been discussed.

Only a few instances of predation on juvenile manini have been encountered incidentally and are presented here briefly. Juvenile manini have been found in the stomachs of moray eels (Muraenidae). A small lizard fish (Synodidae) was observed to catch a juvenile manini in its jaws in shallow water in Kaneohe Bay, Oahu. The manini was too large to be swallowed, and it eventually escaped. A 50 mm. specimen of *Antennarius* was placed in an aquarium with six juvenile manini. A half hour later it had eaten one of them (length, 31 mm.).

In the Society Islands a juvenile *Caranx melampygus* about 90 mm. long was observed from shore to capture a small *Acanthurus triostegus triostegus* 25–30 mm. in length. This carangid occurs in the Hawaiian Islands where it probably feeds in part on manini, as may other species of *Caranx*.

Also in the Society Islands, the young *Acanthurus triostegus triostegus* have been found in the stomachs of the groupers *Epinephelus merra* and *Cephalopholis argus* and the snapper *Lutjanus vaigiensis* (Randall and Brock, 1960).

It is believed that predation (man excluded) on the juvenile stage of the manini in the Hawaiian Islands is much more pronounced than on the adult stage. In addition to the fishes mentioned above, holocentrids, scorpaenids, cirrhitids, and sphyraenids, and possibly also certain

TABLE 2

SALINITY TOLERANCE OF *Acanthurus triostegus sandvicensis*

NO. OF FISH	STANDARD LENGTH (mm.)	CHLORINITY (0/00)	NO. SURVIVING 24 HR.	MAXIMUM HR. SURVIVED
3	26–29	1.4	3	
4	26–29	0.7	0	5
3	27–29	0.1	0	less than 5
1	92	1.4	1	
1	89	0.7	0	8
2	86–90	0.4	0	between 3 and 15
3	27–29	34.8	2	
4	26–28	35.7	2	
3	28–29	37.4	2	
4	26–29	38.25	0	5
1	83	38.25	0	17.5

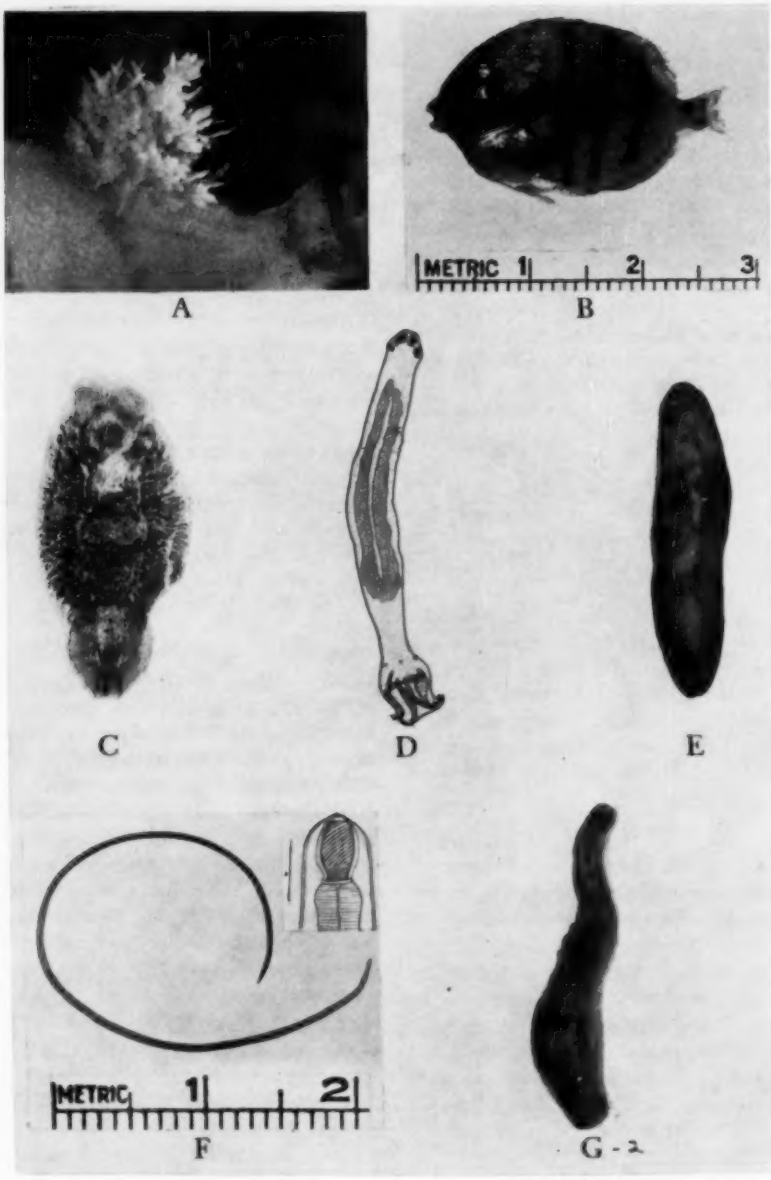

FIG. 2. Parasites of *Acanthurus triostegus sandvicensis*. *A*, Colony of *Hydrichthys* sp. on the dorsal fin of a manini in its first day of transformation from the acronurus to the juvenile state. *B*, *Hydrichthys* on the post-orbital part of the head of a manini in its second day of transformation. *C*, *Benedenia* sp. from the epidermis of an adult manini; length of trematode, 1.9 mm. *D*, *Ancyrocephalus* sp. from the gills of manini; length of trematode, 0.63 mm. *E*, *Hapladena varia* Linton from the duodenum of an adult manini; length of trematode, 2.9 mm. *F*, Adult female *Spirocamallanus monotaxis* Olsen from the intestine of adult manini; insert shows anterior end of the nematode (after Olsen, 1952); red in life, the females attain a length of about 45 mm. and the males about half this size. *G*, Unidentified leech (possibly *Johanssonia* sp.) from the gills of a manini; length of leech, 2.4 mm.

of the larger nocturnal crabs, may feed on small manini. Once a manini reaches adult size, it probably enjoys freedom from predation by most of these fishes in Hawaii, for the inshore marine fauna is peculiar in the paucity of moderately large carnivorous fishes. Shallow-water serranids and lutjanids, many of which are well adapted to prey on reef fishes, were almost totally lacking in the Hawaiian Islands until the recent effort to introduce some of these fishes. The larger native predaceous fishes, such as adults of *Caranx*, *Sphyraena*, and sharks, are not numerous at the present time, probably because of fishing pressure.

PARASITES

Seventeen species of parasites were detected on and within the manini.

Seven specimens of transforming manini were found to be parasitized by *Hydrichthys* (Fig. 2*A*), probably *H. mirus* Fewkes. This unusual hydroid occurred on the head, body, and fins and apparently does not have a preferred attachment site. It was never seen on juveniles or adults. Probably it flourishes only on postlarval manini, for it appears to be abraded and regressing on most of the transforming fish (Fig. 2*B*).

Three specimens of a monogenetic fluke (*Benedenia* sp.) were discovered on the epidermis of two adult manini. The flukes are small (less than 2 mm. in length), perfectly transparent in life, and were hidden in the slime of the fish. They are difficult to find and are probably more common than the few specimens would indicate. Figure 2*C* is a photograph of a stained specimen. Jahn and Kuhn (1932) have worked out the life cycle of *Benedenia melleni*.

The most common fluke of the manini is an unidentified species of the gyrodactylid genus *Ancyrocephalus*. Figure 2*D* is a drawing of a living specimen, 631 micra in length, which was obtained from the gills of a 132 mm. manini. This very small species of trematode was found on the gills of most of the manini which were examined. In some of the manini the infestations were heavy, an average of about one fluke per gill filament being present. It is extremely active and highly extensible and was observed to change its position on a gill filament by attaching with the anterior end and looping the posterior end over to another location where the hooks were dug into place. Siwak (1931) reported on the life cycle of a species of *Ancyrocephalus*.

Two digenetic trematodes were found in the digestive tract of the manini, *Hapladena varia* Linton and *Haplosplanchnus obtusus* (Linton), previously known only from the surgeonfishes *Acanthurus hepatus* (= *chirurgus*) and *Acanthurus coeruleus* at Tortugas, Florida. Manter (1955: 76) included a discussion of this distribution in a recent paper reviewing the zoogeography of trematodes of marine fishes.

Hapladena varia (Fig. 2*E*) was only occasionally found in the intestine of the manini. A total of 22 specimens, usually less than 3 mm. in length, were taken from 200 manini whose digestive tracts were examined for parasites. The manini harboring the flukes ranged from 43 to 136 mm. in standard length.

Haplosplanchnus obtusus was found only in juvenile manini, although it may have been overlooked in adults. It is smaller than *Hapladena varia*, usually less than 1.3 mm., and not as slender. Some of the juvenile manini contained a large number of these flukes. Seventy-one were counted in one 49 mm. specimen. Most of the flukes were in the duodenum, a few extended as far back as the halfway point of the intestine, and a few were found in the pyloric caeca.

Four different nematodes were found in the manini. Two could not be identified to genus. One of these was a very attenuate immature male from suprapharyngeal tissue of the fish. The other was represented only by larval specimens from the pyloric caeca. A third worm, which was occasionally found encysted in the mesenteries, was considered to be the immature female of an unidentified species of *Contracaecum*.

The fourth nematode, *Spirocamallanus monotaxis* (Fig. 2*F*), was described by Olsen (1952) from the sparid fish *Monotaxis grandoculis*, reportedly a mollusk-feeder. In all probability this roundworm will be found in other Hawaiian fishes.

Of 200 manini (mostly adults) from Oahu examined throughout the year for internal parasites, 76 were found which harbored *S. monotaxis* in the intestine or pyloric caeca. The av-

erage number of worms found in these 76 fishes was 5. The largest number of worms in a single fish was 35. No obvious variation of the degree of infestation of this nematode in the manini was observed during the year.

Two different leeches were found on the manini. Both are species in the family of Pisicolidae (possibly genus *Johanssonia*). One is represented by a single 2.4 mm. immature specimen (stained and photographed herein as Fig. 2*G*) which was taken from the gills of an adult manini. Six specimens of the other leech were collected from the body surface of three juvenile manini, 26–31 mm. in standard length, taken in the Ala Wai Yacht Basin on April 17, 1955. These leeches varied from 2.9 to 7.5 mm. in length, were dark brown in life, and easily detected on the host.

Six species of parasitic copepods have been taken from the body surface and pharyngeal cavity of the manini. *Lepeophtheirus dissimulatus* Wilson was the species most commonly encountered: 112 of 164 adult manini examined for parasites throughout the year were infested with from 1 to 20 of these copepods. The other parasitic copepods found were two species of *Caligus*, a *Dentigryps* sp., *Peniculus minuticaudae* Shiino, and *Nessipus costatus* Wilson, which encysts in the fins. A comprehensive report on these and other parasitic copepods from Hawaiian acanthurid fishes is being prepared by A. Lewis.

A mutualistic association was observed between the manini (and other reef fishes) and a small colorful wrasse, *Labroides phthirophagus* Randall. In the clear water off Manana Island two adult manini were seen being pecked over the head and body by this wrasse. The manini remained motionless in the water except for slight undulation of the fins. Since the stomach contents of several of the wrasses consisted primarily of calagoid copepods, it is believed that the fish were removing crustacean ectoparasites from the manini. On another occasion a manini was observed to swim directly to the "domain" of two of these labrids. As the manini was approached by one of them the surgeonfish was speared and brought ashore. Two adults of *Lepeophtheirus dissimulatus* were visible on its body.

DISEASES

The only data on disease were obtained from a series of unsuccessful attempts to maintain manini in an aquarium. Four adult fish were placed in a 23 gal. stainless steel aquarium which had previously been used to keep adult and juvenile manini for periods of several weeks. The water was aerated and filtered. Two days later two of the fish died, and on the following day the remaining fish were dead. Several hours before their death the manini swam in a disoriented manner. The fins were badly eroded. The head and body were excessively slimy, and large scattered sores were present. The fish were examined for parasites and found to have no more than the average complement.

The tank was cleaned (but not sterilized) and two more adult fish added. They died in a similar fashion in 48 hr. The tank was again cleaned and a 57 mm. juvenile manini placed in it. This fish died just 48 hr. later.

In spite of the filtration, the tank became cloudy on the second day after cleaning. A milliliter of the water was taken, successive dilutions made, and the higher dilutions cultured with a sea water and agar mixture (sterile aged sea water, agar, and a small amount of peptone and ferric phosphate). The number of resulting bacterial colonies were counted; the bacterial count of the original milliliter of aquarium water was computed at 212,000,000. Before the fish were placed in the aquarium the number of bacteria were probably less than 1,000,000 per ml.

Several smears were taken from eroded areas of dying manini. The dominant organism was a short, plump, gram-negative rod. It is not known whether this is the etiological agent of the disease or merely a secondary bacterium.

FOOD HABITS

Food of Larval Manini

Only three specimens of larval manini (6.6–7 mm. in total length) were available for an analysis of gut contents. Two of these fish were taken in a plankton net towed between 5:46 and 6:48 A.M. One was empty and the stomach of the other contained two appendicularian tunicates and a larval polychaete. The third fish

was captured between 3:20 and 4:25 A.M. and was empty.

The digestive tracts of 57 manini in the acronurus stage (see section on transformation), which were obtained at night light stations in the Hawaiian Islands, Line Islands, and Phoenix Islands, were examined in the same way. Forty-five were completely empty. Four contained one to seven tiny fish scales; one of these also contained a shrimp chela. A few crustacean appendages (mostly from shrimp) were found in three other fish, one of which had also eaten a barnacle metanauplius. The intestines of two fish had a small amount of unidentified chitinous remains. The crustacean appendages, metanauplius and fish scales were not free in the gut lumen but were caught between longitudinal folds of the gut. It seems evident that the acronuri do not feed at night.

Four acronuri of *Acanthurus* were obtained from the stomachs of skipjack (*Katsuwonus pelamis*) caught during the day in Hawaiian waters. Because of their being partially digested, I am not able to identify any of these acronuri to species; two, however, are too large to be manini. The stomachs and intestines of all four of these fish were filled with zooplankton. Shrimps and shrimp larvae were the principal food items. Also found were copepods, polychaetes, and the remains of larval fish.

Food of Transforming Manini

In an aquarium, manini in their first day of transformation from the acronurus to the juvenile stage were not observed to feed. The digestive tracts of 30 specimens, collected in tide pools during the morning of their first day of transformation and preserved immediately, were devoid of food material. Of 24 similar specimens collected in the afternoon, 19 were empty, but 5 had eaten small amounts of fine filamentous algae and leptopel (for a discussion of leptopel see Fox, Isaacs, and Corcoran, 1951). Second-day transforming manini were seen to feed on algae in an aquarium, though not frequently, and preserved specimens of the same transformation age all contained small amounts of algae and leptopel. During the remaining 2 or 3 days of transformation, feeding is progressively heavier.

Food of Juvenile and Adult Manini

The gut contents of juvenile and adult manini consist almost entirely of relatively fine filamentous algae. The teeth of the manini are close-set and denticulate on the margins (Randall, 1956 *b*: fig. 2a) like other species of *Acanthurus*. They are therefore well adapted for feeding on filaments of algae. Experiments on feeding in aquaria showed that the absence of coarser algae in the gut contents is due to limitation in the size and strength of the jaws and teeth. Only the smaller branches of coarser algae, like species of *Hypnea*, were eaten. Small juvenile manini only ate the fine end branches whereas larger fish ate progressively larger branches.

Inorganic sediment was rarely found in the stomach or intestines of manini. When branches of a delicate species of the red alga *Polysiphonia* were mixed with fine sand and offered to aquarium manini, the fish were most adept at picking out the filaments which projected above the sand. The stomach of the manini is thin-walled, similar to that figured and described by Breder and Clark (1947: 295, fig. 1) for *Acanthurus coeruleus*. It contrasts sharply with the thick-walled, gizzard-like stomachs of some species of *Acanthurus*. Unlike the manini, the latter species normally ingest large amounts of inorganic sediment with the algae upon which they feed.

In addition to avoiding the ingestion of inorganic debris, juvenile and adult manini do not seem to feed on animal material (although some species of *Acanthurus*, such as *A. xanthopterus*, will accept animal food readily). Even when hungry, manini declined to eat any of several kinds of animal food which were offered. In an aquarium the fish were very skillful in avoiding the intake of small crustaceans and small masses of tunicates or sponges which were in close proximity to the algae on which they were feeding. Occasional small animals are found in the gut contents, however. These are probably taken in accidentally. In shallow water at Coconut Island, Oahu, an adult manini was observed feeding on algae close to an egg mass of the damselfish, *Abudefduf abdominalis* (the guarding fish had been frightened away). When the manini reached the edge of the egg mass, it ceased to feed, swam over the mass, and began feeding on algae on the other side. Other fishes,

such as labrids and chaetodonts, feed greedily on the eggs when afforded the opportunity to do so by the absence of the guarding parent.

A study of the kinds of filamentous algae eaten by manini was undertaken. It was soon apparent that a great many different species of algae are eaten, and it is believed that at least a few filaments of virtually every filamentous alga in the Hawaiian area can ultimately be found in the gut of the manini if enough specimens are examined.

Dawson, Aleem, and Halstead (1955: 21), reporting on the gastrointestinal contents of 42 *Acanthurus triostegus triostegus* (size of specimens not given) from Palmyra, Line Islands, found 40 species of benthic algae and a number of species of diatoms of several genera. The number of algal species exceeded that previously known from Palmyra. Five species were most common in the stomachs: *Pterocladia* sp., *Sphacelaria furcigera*, *Lyngbya majuscula* (and/or *L. aestuarii*), *Bryopsis pennata*, and *Lophosiphonia* sp. The authors assumed that these were either dominant algae in the grazing grounds of the fish or were especially selected as food. It is the opinion of this author that these are the dominant algae, for (as is discussed below) the blue-green *Lyngbya majuscula* and another *Lyngbya* are not selected by this surgeonfish (at least not the Hawaiian subspecies).

A simple piece of apparatus was devised to test the preference by manini in Hawaii for various kinds of common filamentous algae. Ten tongue depressors were attached 2 cm. apart to a piece of wood. The free end of each depressor was notched and wrapped with a short piece of pliable galvanized steel wire. Different kinds of algae were fastened to the depressors by wrapping the wire ends around them. All 10 depressors with the assortment of algae attached were lowered simultaneously into the center of an aquarium in which juvenile manini, 26–30 mm. in standard length, were kept. When experiments were repeated, the position of the algae was always changed. If an alga was not eaten during the course of the experiment, it was left in the aquarium as long as it appeared edible to see if it would ultimately be devoured. The results are given in Table 3.

Many of the above algae were offered in a comparable manner to two adult manini, 123 and 128 mm. in standard length, with similar results.

Some species of algae not listed in the table were offered but not eaten; these, however, were probably too coarse for the juveniles. Included were two species of *Laurencia*, a species of *Gelidium*, a *Gracilaria*, and a species of *Dictyota*. A thallus of one of the species of *Laurencia* was placed in the aquarium with the adult manini. The small branches were eaten, leaving the major branches denuded.

Of the seven kinds of algae fine enough to be eaten but ignored in the preference experiments, one is a red (*Asparagopsis taxiformis*, well known for its high iodine content), one is brown (*Ectocarpus breviarticulatus*), and the rest are blue-greens. These were the only blue-greens tested.

Blue-green algae, some of which are the same species as those in the preference experiments, have been found in the stomachs and intestines of manini by the author (and, as noted, by Dawson, Aleem, and Halstead, 1955). This seems inconsistent with the results of the experiments. It was noted, however, that the blue-greens were never the exclusive food material, but were always mixed with large amounts of other algae, usually reds or greens.

In May, 1952, in water 10–20 ft. deep in Hanauma Bay, Oahu, the bottom was examined for the kinds of fine algae which reach a height of about 5 cm. or more. Three species this size were common: *Lyngbya majuscula*, *Asparagopsis taxiformis*, and *Plocamium sandvicense* (a red alga). Since surgeonfishes are abundant in the bay and at least two of the three algae are distasteful to one surgeonfish, the success of these algae might be associated with distasteful qualities.

Although there was little question from the observations that the manini requires no animal food, an experiment was designed to demonstrate that this species can subsist and grow on algae alone. A 23-gallon aquarium was divided into two compartments with a piece of plexiglass. Six manini, 26–31 mm. in standard length, were placed on each side and provided with cover in the form of several rocks grouped in the center of each compartment. The fish on one

TABLE 3

PREFERENCE FEEDING EXPERIMENTS ON JUVENILES OF *Acanthurus triostegus sandvicensis*

PREFERRED	COMPLETELY EATEN	SPARINGLY EATEN	NEVER EATEN
Polysiphonia sp.	*Hypnea* sp.	*Ectocarpus indicus*	*Lyngbya majuscula*
Enteromorpha sp.	*Hypnea* sp.	*Sphacelaria* sp.	*Lyngbya* sp.
	Lophosiphonia sp.	*Liagora* sp.	*Hormothamnion enteromorphoides*
	Ceramium sp.	*Jania* sp.	*Hydrocoleum cantharidosmum*
	Centroceras sp.	*Rosenvingia* sp.	*Calothrix confervicola*
	Gracilaria sp.	*Trichogloia* sp.	*Ectocarpus breviarticulatus*
	Rhizoclonium sp.	fixed diatoms (many species)	*Asparagopsis taxiformis*
	Dasya sp.		
	Enteromorpha sp.		
	Cladophora sp.		
	Grateloupia sp.		
	Herposiphonia sp.		
	Microdictyon setchellianum		

side were fed with a *Polysiphonia* and those on the other with an *Enteromorpha* (these were the algae upon which manini fed most vigorously in the preference experiments).

These algae are among the first macroscopic organisms to appear on the bottom of boats in harbor areas on Oahu. They are fast growing, especially the *Enteromorpha* which increased its length an average of 27 mm. per day on the eastern side of a boat during a period of 5 sunny days in April. If collected when the thalli first develop, they are almost devoid of animal life. A fresh mass of the *Enteromorpha* weighing 1.75 g. contained one ciliate, one nematode, one copepod, and a few epiphytic pennate diatoms and blue-green algal cells. Nevertheless the algae were thoroughly washed and picked over for animals before being fed to the fish. Fresh algae were added to the aquarium every day, and the previous day's algae removed. At the end of 2 weeks the fish were measured. Those fed on *Polysiphonia* grew an average of 2.9 mm.; those fed on *Enteromorpha* grew an average of 3.1 mm. During the 2-week interval the temperature in the aquarium was cool, varying from 23.0° to 23.8° C.

The preference experiments indicated that neither of these algae was eaten more readily than the other. Manini often alternated between feeding on the two. After 2 weeks of feeding on one of these, both kinds were added at the same time. It was immediately apparent that the fish had been conditioned to the alga on which they had been feeding. The "new" alga was untouched initially and only occasionally sampled an hour later. The preference was no longer obvious by the end of the day, however.

Manini feed almost constantly during the day, both in an aquarium and their natural habitat. They do not feed at night (see section on behavior).

The volume of algae consumed is large. Four juvenile manini, 28.5–45 mm. in standard length and weighing a total of 8.3 g., were fed a known mass of *Enteromorpha* in an aquarium early in the morning. The alga was weighed after firm squeezing followed by blotting on paper towels. At the end of the day the remaining fresh algal material was weighed in the same manner. Fresh *Enteromorpha* is grassy green and can easily be distinguished from fecal alga which is brownish or blackish green and tends to remain in pellets. The manini ate 10.8 g. of this alga one day and 8.8 g. the next. The same procedure was utilized for two adult fish, 123 and 128 mm. in standard length and 83.2 and 94.5 g. in weight, respectively. These two fish ate 27.4 g. of *Enteromorpha* in one day. The second day 16.3 g. of *Polysiphonia* was consumed. After being unfed during the morning of the third day, they ate 25.2 g. of *Enteromorpha* during the remaining 6 hr. of the day. Although these two adult manini in the above experiment were well adapted to aquarium life (they were reared to this size as captive fish in a pond of the Hawaii Marine Laboratory at Coconut Island and were

maintained in the aquarium 12 days before the experiments), it was observed that they did not feed as frequently as adult manini in the natural environment (whereas the juveniles did). The feeding by the adults was readily interrupted by the approach of an observer. Usually only one fish fed at a time, and since the larger one dominated the smaller and held it in a corner of the aquarium for much of the day, the former consumed the major part of the algae. Yet both fish disdained to feed at all when placed in separate aquaria.

Stimulus to Feeding

The following simple experiments and observations were conducted in order to ascertain what sensory mechanism or mechanisms are utilized by the herbivorous manini in finding food.

The juice from several grams of *Enteromorpha* was squeezed into an aquarium in which two adult manini had been starved for a day. This was unfiltered and colored the water green when first dropped into the aquarium. No response was observed, even when some of the green color was seen to diffuse in the immediate vicinity of the nose and mouth of the fish. A similar experiment was performed on several juvenile manini with *Polysiphonia*, again with no visible response. By contrast, when an extract of *Polysiphonia* was dropped into an aquarium containing a half-grown *Abudefduf abdominalis* (omnivorous in food habits), this fish swam to the surface where the extract clouded the water red and snapped its jaws erratically in this region.

Some *Enteromorpha* and *Polysiphonia* was boiled to the extent that the algae began to disintegrate and lost most of their color. This was placed in the aquarium with fresh algae of the same kinds. Although juvenile manini fed initially on the fresh algae, the boiled algae was ultimately completely eaten.

Some maroon rayon fiber similar in texture and color to *Polysiphonia* was placed in an aquarium with juvenile manini. It was taken into the mouth temporarily by several of the fish. When the rayon was soaked in extract of the *Polysiphonia*, it was not taken in with greater frequency.

When recently voided fecal *Enteromorpha* was placed at the surface of the aquarium in the same manner that fresh algae were offered, most of the manini approached it, hesitated, and swam away. One juvenile drew a small amount into its mouth but hastily ejected it. When defecated filaments were added together with fresh filaments of *Enteromorpha*, only the fresh alga was eaten. In the absence of fresh algae, fecal algae which have remained in the aquarium for several hours may be ingested. The results of offering the blue-green algae listed in Table 3 were similar to that just described for recently voided fecal algae. The blue-greens were approached, but rarely taken into the mouth.

The nasal organs of a 26 mm. manini were cauterized with a hot wire. Five min. after this, the fish was offered some *Polysiphonia*. It fed on this with the same "enthusiasm" as previously.

Another juvenile fish was blinded by wiping a crystal of potassium hydroxide over the eye (other fish were blinded with silver nitrate crystals but these invariably died within 36 hr.). After contact with the potassium hydroxide, the surface of the eye became opaque white; this fish survived more than 3 days. It moved slowly about the bottom, occasionally swimming by chance into a mass of *Polysiphonia*. It never swam directly to the algae. When the algae touched the mouth it was often eaten. By the third day when the aimless movements carried the fish into a mass of algae, it fed voraciously.

It is concluded from the above that vision alone is needed to locate algal food, and the olfactory sense functions in feeding only to avoid unsavory material. Chemoreceptor organs in the mouth and possibly tactile organs as well also seem to be associated with the acceptance of algae and the rejection of material which is not utilized as food. The tendency to feed more on one alga than another develops after the algae have been sampled.

DIGESTION

In the work on nutrition of marine animals much effort has been expended on the analysis of mode of feeding and stomach contents, whereas little has been applied to the important

aspect of the digestion of these animals. Yonge (1931) pointed out that information as to what an animal may collect and pass into its alimentary system may or may not indicate the true food of the animal. Thus, a study of digestion should logically accompany an investigation of food habits. The author is especially indebted to P. B. van Weel of the University of Hawaii for his counsel in the following research on digestion.

Morphology of the Digestive Tract

The similarity of the stomach of the manini to that of *Acanthurus coeruleus* as described by Breder and Clark (1947) has been mentioned. The manini stomach is elongate, and divisible into cardiac and pyloric portions. The cardiac part has prominent, longitudinal, irregularly scalloped folds on the inner surface; the pyloric part is smooth. A cross-section of the pyloric part showed the muscle tunic to be about the same width as the mucosa. There are few multicellular glands. The stomach wall is less than 0.1 mm. thick except posteriorly near the pylorus where it is slightly thicker than 1 mm.

Just posterior to the pylorus are five pyloric caeca. Several authors (including Yonge, 1931) have claimed that the pyloric caeca has taken over the role of the pancreas in certain teleosts, the latter organ supposedly being absent in these fishes. Dawes (1929) found that the pyloric caeca of the plaice (*Pleuronectes platessa*) had the same structure as the intestine with which it was in free communication, and Rahimullah (1945) came to the same conclusion after examination of 119 species in 50 different families of fishes. The structure of the pyloric caeca of the manini is consistent with the findings of Dawes and Rahimullah. The bile duct opens into the base of one of the pyloric caeca.

The pancreas of the manini was difficult to find. It was finally located in the form of two to four (usually three) small, round glands buff in color lying in the mesentery alongside the bile duct near its junction with the liver.

The intestine of the manini is long, in keeping with the well-founded biological principle that herbivorous animals have lengthy intestines. The length of the alimentary tract of large adult manini is nearly six times the standard length of the fish. Most of this length is attributable to the intestine which is complexly folded within the body cavity. The length of the alimentary tract of small juvenile manini is only slightly greater than three times the standard length of the fish. The increase of the alimentary tract relative to standard length is shown in the graph of Figure 3. With increasing size the volume of a body requiring nutriment increases faster than the intestinal surface if the rate of growth of the two is equal. A disproportionate elongation of the intestine is necessary to keep the area of absorptive surface adequate to the needs of the body. Hiatt (1947: 254, 257) noted a striking increase in the relative growth of the intestine of the herbivorous milkfish (*Chanos chanos*) between 90 and 115 mm. standard length. The ratio of intestinal length to standard

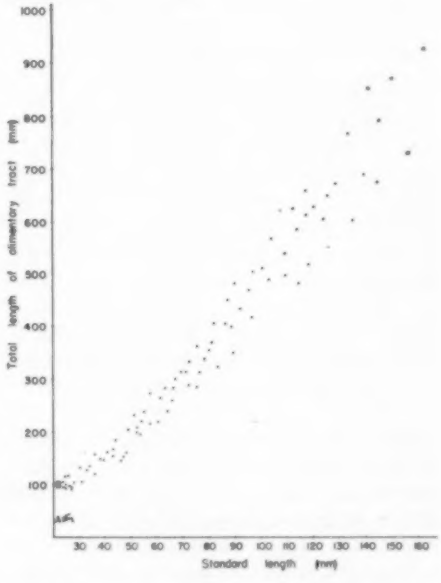

FIG. 3. Change in length of the alimentary tract of *Acanthurus triostegus sandvicensis* with increase in standard length. The group of points at *A* represents the length of the tract of 10 specimens (24–27.5 mm.) in the acronurus stage which were taken at a night light offshore. The points at *B* represent 10 tide-pool specimens (24–28 mm.) which have just completed transformation from the acronurus to the juvenile stage.

length increased from 3.5:1 to 7.2:1. He demonstrated a correlation between the increase in length of intestine and the substantial rise in the amount of larger algal types in the stomach contents and the reduced number of smaller food items like diatoms and blue-green algae. No sudden change-over in the size of algal food which is eaten by the manini occurs at any size range once transformation has taken place, and the curve of alimentary tract length plotted against standard length is without sharp inflection. The great increase of the gut length which occurs when manini transform from the acronurus to the juvenile state is discussed in the section on transformation.

The inner surface of the intestine is covered with small villi. The wall of the intestine is thin, its average thickness, not including any villi, is about 0.05 mm. The mucosa is about three to four times as broad as the muscle tunic.

Time for Algae to Pass through Gut

In order to find out the time which is required for algae to pass through the entire alimentary canal of the manini, two adults, 123 and 128 mm. in standard length, were fed only the red alga, *Polysiphonia*, for a period of 2 weeks. The tank was cleaned and the diet switched to the green alga, *Enteromorpha*. Two hr. and 25 min. later the fish were observed defecating the green alga. They had already deposited some on the bottom of the aquarium, so the following day the experiment was repeated by switching back to the red alga. In 2 hr. and 4 min. the first of the red alga was voided. In view of the great length of the digestive tract, this short interval of time seems extraordinary. However, when considered in the light of the nearly constant diurnal feeding and the volume of algae consumed, it becomes more understandable.

The same procedure was repeated for small juvenile manini, ranging from 26 to 30 mm. in standard length. The *Polysiphonia* passed through their alimentary tracts in 1 hr. and 45 min.

At night, when feeding ceases and the fish enter a state of torpor, the gut is not completely emptied in 2 hours or so. One 39 mm. manini, for example, which was caught at 1:15 A.M. still had a small amount of algae in the stomach and in the last 26 mm. of the intestine. The total length of the alimentary tract of this specimen was 177 mm. A 123 mm. manini was observed to defecate *Enteromorpha* 14 hours after it last fed on this alga.

Digestion of Algae

Lefèvre (1940) has shown that different kinds of algae resist digestion by gastrointestinal juices of fishes in various degrees. Although supporting growth of manini as well or better than the *Polysiphonia*, the *Enteromorpha* appeared less digested. Filaments of this alga were found to be only slightly altered after their rapid passage through the gut. The cellulose cell walls seemed unaffected, and the cell contents still in place. The only discernible change in most cells was the breaking up of the parietal grassy green chloroplast to brownish-green granular clumps. A visual comparison was made of the quantity of starch granules in the *Enteromorpha* cells following staining of fresh and fecal algae, and no obvious differences were apparent. Clearly, more work is needed to elucidate the problem of algal nutrition of the manini. The possibility that the pectic sheath material of algae is digested should be investigated.

Digestive Enzymes

No reference was found in the literature to any assay of the digestive enzymes of a strictly herbivorous fish. From work on herbivorous animals other than fishes the generalization can be made that proteinase is less active in herbivorous forms than in carnivores and amylase more active. There are indications that this is true for fishes, at least for amylase. Kenyon (1925) compared starch digestion in the carp (*Cyprinus carpio*) which, though omnivorous, eats large amounts of algae, and the carnivorous pike (*Esox lucius*). He wrote, "... the carp, which is largely a vegetarian, possesses amylase in tremendous amounts in the hepatopancreas and to a less extent throughout the intestinal mucosa. The pickerel, on the contrary, ... possesses only a negligible quantity of amylase, having little in the pancreas, esophagus, intestine, and practically none in the stomach." Vonk (1927)

wrote that the carp has more than 1,000 times the amount of amylase in the pancreas than that of the carnivorous pike or shark. Schlottke (1939) found amylase in large quantities in the carp, whereas the predaceous rainbow trout (*Trutta iridea*) and perch (*Perca fluviatilis*) evidently produced almost no amylase. Data comparing the activity of proteinase and lipase of omnivorous and carnivorous fishes are meager and conflicting.

In view of the importance of the hydrogen ion concentration to enzyme activity, the pH of the contents of various parts of the digestive system of the manini was determined. The measurements of pH were made with a Beckman pH meter on six adult fish which averaged 120 mm. in standard length. The results, expressed in the ranges of pH found, are given in Table 4.

TABLE 4

pH OF ORGANS OF THE DIGESTIVE SYSTEM OF *Acanthurus triostegus sandvicensis*

ORGAN	RANGE OF pH
Stomach	6.3–7.7
Duodenum	7.7–9.1
Intestine	8.0–9.1
Gall bladder	6.2–6.4

The variation of pH within any one organ appears to be correlated with the degree of fullness of the organ. The low pH values were found in the organs when they were filled with algae. Hydrochloric acid secretion in a stomach in which food is present is a probable explanation for the greater acidity at this time. Babkin and Bowie (1928) found a variation in pH of the duodenum of the killifish (*Fundulus heteroclitus*) similar to that shown above for the manini. These authors also noted that low values of pH were obtained when the duodenum contained food. They attributed this to the discharge of bile to the organ when filled with food.

Extracts for the enzyme study were consistently prepared from the stomach (both cardiac and pyloric portions combined), pancreas, pyloric caeca, duodenum, and intestine of adult manini which were killed immediately before the removal of these organs. Because of the excessive thinness of the gut wall, it was very difficult to separate the mucosa from the muscle layers; therefore extracts were made of entire organs or linear parts of organs. All portions of the digestive tube to be extracted were first washed with sea water to remove food material. Tissues were ground in mortar and pestle with calcareous sand. This sand had previously been cleaned by repeated washings with water, boiling with 3 per cent potassium hydroxide and then for a short while with 2 per cent hydrochloric acid. In view of MacKay's (1929) report that 30 per cent alcohol yielded the most active amylase from the eel pout (*Zoarces anguillaris*), this agent was also used to extract amylase in the present study. Lipase extracts were made in 40 per cent glycerol and protease extracts in 50 per cent glycerol. Extraction was carried out in a refrigerator for a period of 24 hr.

Digestion by amylase and lipase proved to be rapid at room temperature (26°–27° C.); thus no incubation was necessary in experiments with these enzymes. Digest tubes with protease were incubated at 36° C.

Buffer solutions used in the digestion experiments were based on the mixtures of Clark and Lubs (Hawk and Bergeim, 1942: 24). Bacterial action was prevented by the addition of several drops of toluol to the extract and digest test tubes.

The substrate for amylase experiments was 1 per cent starch solution. To each test tube containing 1 ml. of extract of the digestive organs 5 ml. of starch solution and 1 ml. of buffer of pH 6.8 were added. For each tissue there was a control tube identical with the experimental digest tube except for the previous boiling of the extract to inactivate all enzymes.

The progress of digestion was followed by removing small amounts of fluid from the digest tubes and testing with Lugol's solution. The changes in the solution from deep blue-black through purple, red, yellow, and finally colorless indicated a breakdown of the starch at least to achroodextrine. Ultimately all of the tubes were colorless, thus disclosing starch digestion by the pancreas, pyloric caeca, duodenum, intestine, and stomach. The experiment was repeated three times with sections of the digestive tract vigorously washed to minimize the possibility of enzyme from another source being adsorbed on the epithelial surface of the organ being tested.

Again, there was a definite amylase reaction from each organ.

The positive results seem unusual in view of the fact that most vertebrates (except for mammals which secrete ptyalin in their saliva) break down starch initially with pancreatic amylase and complete the process with intestinal maltase. These results on the manini seem less dubious, however, in the light of the finding by Kenyon of amylase throughout the whole gut of the carp (although it was considered to lack a true stomach) and by the detection of stomach and duodenal amylase in *Zoarces* by MacKay. Also Babkin and Bowie found amylase in the intestine of the killifish. They were certain it was not adsorbed pancreatic amylase, for they were unable to observe any proteolytic action in the same extract.

Pancreatic amylase of the manini is nearly 20 times more powerful per unit of tissue than the amylase from other organs, while that from the stomach was weakest (attempts were made to obtain extracts from equal amounts of glandular tissue of the organs under comparison).

The pH optimum of the amylase, as determined by color change with Lugol's solution and the micro method of Linderstrøm-Lang (Linderstrøm-Lang and Holter, 1933), is 6.7.

The Schoorl method was utilized to test for the presence of maltase in the stomach, pyloric caeca, pancreas, duodenum, and intestine of the manini. One per cent maltose solution served as the substrate. Trials for all organs were run at pH 7.0 and 7.2 and incubated at 30° and 35° C. for periods up to 12 hr., but results were consistently negative.

The method of Michaelis and Rona (see van Weel, 1937: 245) was used in lipase experiments. Tri-n-butyrin solution was used for the substrate. Digestion occurred rapidly in all the organs tested. It was evident that the pancreas produced the most lipase and the stomach the least, although the difference was not as marked as with amylase. The pyloric caeca showed the greatest lipase activity of the remaining organs. Difference between the duodenum and the rest of the intestine was not discernible. The pH optimum determined for pyloric caeca lipase of the manini is 7.2.

Detection of protein digestion was based on the formaldehyde titration of Sörensen (Jordan, 1927). The substrate was a 3 per cent colloidal solution of gelatin.

In initial experiments protease was found in the pancreas, pyloric caeca, duodenum, and intestine, but not in the stomach. In none of the organs was the proteolytic activity strong. The pH optimum of pancreatic protease is 8.4.

Because of the acidic reaction in the stomach of the manini and the knowledge that protease in this organ can vary widely from individual to individual depending on the state of hunger of the animal (Schlottke, 1939), further effort was expended to localize this enzyme in the stomach. Extract of high concentration (prepared from trituration in 5 ml. of 50 per cent glycerol of three adult manini stomachs, two of which contained considerable algae) finally gave positive results. One ml. of this concentrated extract (thus containing the extractable enzyme from three-fifths of a stomach) at pH 6.0 yielded acid equivalent to 0.2 ml. of 0.015 normal sodium hydroxide after 4 hr. of incubation.

A piece of the very thin covering (one cell layer thick) from one of the internal rings of an onion was peeled off and placed in a glass stender and covered with the fluid from the intestine of an adult manini. The onion skin was examined after 24 and 48 hr. periods, but no digestion of the cellulose cell walls occurred. The experiment was repeated with fluid from the intestine of another adult specimen, again with negative results. Thus there appears to be no cellulase-secreting micro-organisms in the intestine of the manini.

It is concluded that the results of the enzyme study of the manini are consistent with the generalization previously made concerning the digestive enzymes of herbivorous animals except for the absence of cellulase.

REPRODUCTION

Sex Ratio

No sexual dimorphism in external morphology was noted; therefore gonad examination was necessary for sex determination. The gonads lie in the ventroposterior part of the body cavity. No difficulty was experienced in distinguishing an ovary from a testis macroscopically except with immature fish. The ovaries are pinkish

cream in color, smooth, slightly compressed laterally, and closely applied to one another in the mid-line. The testes are white, strongly compressed, irregularly lobular, and in contact with each other only ventrally.

It was apparent from sampling the catch of trap fishermen throughout the year that approximately twice as many male manini as females were taken. In the month of May, 1953, 291 trap-caught adult fish were sexed; 68 per cent of these were males. The traps in which the fish are caught are unbaited. A typical trap consists of a rectangular framework (about $2 \times 5 \times 6$ ft.) of steel rod covered with chicken wire. A cone of chicken wire with a narrow slitlike opening extends inward from one end to about the center. Some trap fishermen prefer to leave one or two butterfly fish or other fishes of little economic value in the trap in the belief that other fishes will be more prone to enter. If male manini are more gregarious or less cautious or more migratory than females, they would be caught in traps with greater frequency than females; therefore sex ratios ascertained from trapped fish should be viewed with caution.

The sex was determined for 221 adult manini from islands in the tropical Pacific in the collections of the U. S. National Museum, the Bernice P. Bishop Museum, and the University of Hawaii. Most of these specimens were taken with rotenone, seine, and throw net. These collective techniques are less selective than traps and the sample would seem to be a better indication of true sex ratio. Of the 221 fish, 134 (60.7 per cent) are females. A chi-square value of 10 results from testing whether 134 females could be obtained from 221 fish randomly sampled from a population in which the true sex ratio is 50-50. This high chi-square has a probability greater than 0.01 that a sample more extreme than the above could be drawn by chance from a half male, half female population; thus the hypothesis of a 50-50 sex ratio is rejected.

It is nevertheless possible that the apparent predominance of female manini is spurious. Most of the 221 specimens were taken in inshore areas. The traps from which 198 males of 291 manini were caught were set in from 30 to 90 ft. of water. Perhaps females are more abundant in shallower water and the males predominate over deeper parts of the reef. More collections are needed to clarify this problem.

The museum collections of manini offer some slight evidence for differential schooling by sexes. One sample of 7 manini from the outer reef at Eniwetok Atoll, Marshall Islands, is entirely male; another of 12 fish from the lagoon of Kwajalein Atoll in the Marshalls is wholly female.

Spawning Cycle

The manini in the Hawaiian Islands has a distinct spawning season. This has been ascertained by the examination of the gonads of adult fish and collections of young throughout the year. In more equatorial areas, on the contrary, the spawning of this surgeonfish appears to be year-round. There is also evidence both in Hawaii and the Gilbert Islands that the pattern of the incoming young correlates with the lunar cycle. This is attributed to a lunar effect on spawning by adults.

From October 31, 1952, to October 27, 1953, a total of 137 female and 156 male manini 100 mm. or more in standard length were purchased in 41 samples from a fisherman for the purpose of examination of the gonads. The fish were caught in traps set in depths of 30–90 ft. from Kewalo Basin to Koko Head, Oahu. The length of the gonad on each side of the body cavity of each specimen was measured and the average length recorded. This average measurement was divided by the standard length and the quotient multiplied by 100. The range and mean of the resulting percentages are presented in Table 5.

Although the monthly samples are small, it is nevertheless apparent that the gonads of both sexes undergo a significant change in relative length during the year. They are largest in late winter and spring and smallest in late summer and early fall. The change which takes place in the ovary in late July and August is more complex than would be indicated from a mere shortening. The ovary (presumably following the last spawning) is red, flattened, and has a large lumen. Residual eggs are gradually absorbed (eggs being absorbed appear as amorphous masses of variable size), and the entire organ regresses to small size and a translucent gray color. There is

TABLE 5

GONAD LENGTH AS A PERCENTAGE OF STANDARD LENGTH BY MONTH, 1952–53

MONTH	NO. OF FEMALES	GONAD LENGTH / STANDARD LENGTH × 100		NO. OF MALES	GONAD LENGTH / STANDARD LENGTH × 100	
		Range	Mean		Range	Mean
Oct.	15	7.1–18.2	9.4	14	5.6–22.8	9.4
Nov.	2	7.7–14.4	11.1	12	8.3–22.8	15.5
Dec.	4	12.3–25.0	14.3	11	10.0–22.1	15.9
Jan.	9	8.6–25.6	13.5	10	8.4–25.0	17.9
Feb.	15	14.1–25.6	18.2	31	20.4–34.5	28.6
Mar.	19	13.5–32.2	19.3	25	12.8–35.7	28.6
Apr.	17	10.4–26.4	17.3	7	22.8–38.5	29.4
May	6	9.8–23.3	16.2	5	18.2–31.2	25.6
Jun.	9	7.0–34.5	13.5	5	15.0–25.1	20.0
Jul.	10	7.5–17.6	9.6	9	8.1–26.3	14.9
Aug.	9	5.5–11.9	7.2	8	6.5–23.8	13.2
Sept.	22	5.0–14.5	8.4	19	7.6–17.3	9.0

variation in the time when this occurs in individual fish, hence the ultimate small size is not apparent when the values of a number of fish are averaged by month. The ovary of a 145 mm. female taken on August 7, for example, was only 8 mm. in length.

The gonad measurement data are more significant in indicating a definite spawning season of the manini when coupled with the results of sampling the young throughout the year. Transforming and small juvenile specimens were absent from inshore areas during the fall and early winter months of 1952–53. Extensive observation and collecting were undertaken during the winter and early fall to ascertain the time of the first and last arrivals of acronuri from the pelagic realm. The first transforming young were sighted on February 14; the last of the season straggled in on October 6. In 1954 the first young were discovered on February 9. During my absence from the state, my wife and Philip Helfrich made an effort to determine the date of the last influx of young in 1954. In October only a single small juvenile was collected; it was taken on the 9th of the month and measures 27.5 mm. in standard length. It is completely transformed; therefore it had been in the tide-pool zone for about 5–8 days (see sections on transformation and growth). The first transforming young of the 1955 season were observed on January 27.

The time between the finding of the first ripe female of the season and the first incoming young and the time between the last ripe female and the last incoming young constitute estimates of the duration of larval life. The last ripe female of the 1952–53 season detected in the sampling program (see Table 6) was found on July 21. The first ripe female of the 1953–54 season was found on December 1. The last ripe females of this season were observed in the July 16 sample. The three estimates of the duration of larval life from the above data are 71, 78, and 83 days. Admittedly such estimates are subject to considerable error. Their average, 77 days, approximates 2½ months.

In order to obtain quantitative data on the recruitment of young to inshore areas of Oahu, a single large tide pool at Diamond Head (Fig. 4) was chosen for repeated collections of manini. This pool is nearly isolated at low tide. An overhanging ledge on the left (east) side of the pool provides excellent cover for the small fish. Pools as large as this but lacking such cover contain fewer manini. Each week at low tide the narrow outlet to the sea was occluded with a net, and all the manini in the pool were poisoned with rotenone. A total of 157 manini less than 30 mm. in standard length were taken from the pool during the season (Fig. 5). Nineteen specimens 30 mm. or longer were collected; these are presumed to have been in the tide-pool zone for more than one week (see section on growth) and hence are probably migrants from adjacent pools. They are not included in

FIG. 4. Tide pool at low tide at Diamond Head, Oahu, from which the collections of *Acanthurus triostegus sandvicensis* of Figure 5 were made.

the graph of Figure 5. The poison stations on August 13 and August 21 were interrupted by unexpected large waves, and no fish were collected. However, on these two dates manini were counted in the pool before rotenone was added and these numbers are indicated by the dotted line on the graph. Probably there were at least twice as many small manini in the pool as are recorded, for most of the fish take cover rapidly when an observer approaches and are hidden before they can be counted. The sample of 36 fish taken on September 12, on the other hand, may be higher relative to the overall number of tide-pool young at this time than it should be. Observation of other pools at Diamond Head and along the shore of the Ala Wai Yacht Basin prior to, during, and after September 12 failed to disclose any striking influx of young. Nevertheless, the number of incoming young in September is high and this month should be included with the period May to August as indicating large tide-pool recruitment on Oahu.

Although this sampling from a single pool is not sufficiently great to be correlated closely with the similarly inadequate samples of adult gonads, the May to September recruitment seems to correspond roughly to the greater degree of gonad development from February to June.

In more equatorial waters the *A. triostegus triostegus* appears to spawn throughout the year. The 221 adult fish used for the sex ratio determination were collected mostly from the Mari-

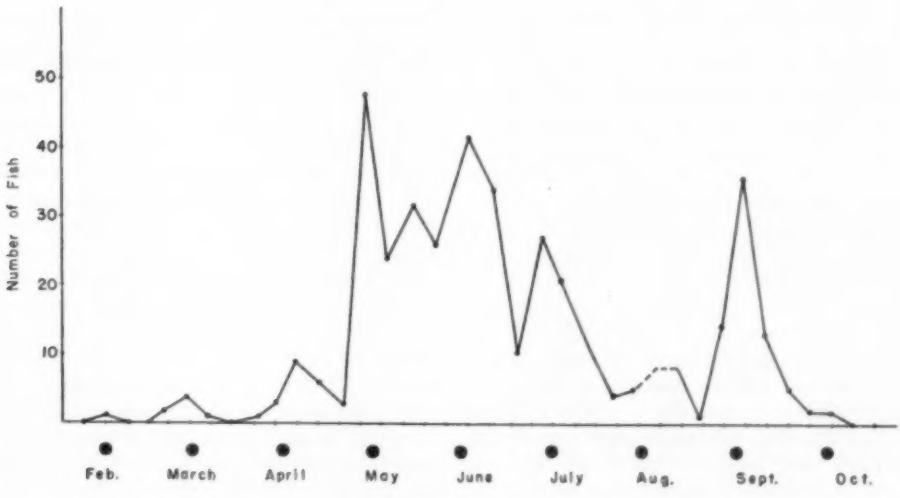

FIG. 5. Weekly collections of *Acanthurus triostegus sandvicensis* made in 1953 from a single tide pool at Diamond Head, Oahu. Only specimens 30 mm. or less are recorded. Times of new moon are indicated by black circles.

ana, Marshall, Gilbert, Line, and Phoenix islands—groups in which the sea surface temperature exceeds 80° F. (26.7° C.) the year-round and where the annual variation in sea temperature is slight (based on Hydrographic Office, 225). Examination of these fish revealed ripe gonads in every month of the year. Specimens of transforming or small juvenile manini collected every month of the year from these areas were found in museums.

It is, therefore, puzzling that the seasonal spawning in the Hawaiian Islands seems to be associated with the colder part of the year. The mean monthly sea surface temperatures around Oahu (1945–55) vary from about 75° to 81° F. in an average year (Leipper and Anderson, 1950; Hydrographic Office, 280.) The temperature of the warm part of the year is essentially the same as that of the lower latitudes where spawning is year-round. The initial enlargement of the gonads in Hawaii coincides with the time of decreasing sea surface temperature in the fall. The marked increase in tide pool recruitment in May appears to correspond to increased spawning in February–March, the time of coldest water temperature.

If temperature or some other factor such as change in length of day is the cause of interrupted spawning in Hawaii, then manini in a region of the South Pacific Ocean with comparable latitude should spawn seasonally and 6 months out of phase from Hawaiian manini. Unfortunately no data are available from southerly island groups such as the Australs or southernmost Tuamotus where sea temperatures closely approximate those in Hawaii.

Small juvenile and transforming *A. triostegus triostegus* were taken or observed by the author in every month of the year (1956–57) in the Society Islands (where temperatures range from about 77.5° to 81° F., or 25.2°–27.2° C.). The manini is not as abundant in the Society Islands as in Hawaii, and the insignificant tide in the former island group made it difficult to find numerous individuals isolated in tide pools. Collections were insufficient to demonstrate any possible variation in reproductive activity during the year.

A cyclic fluctuation in the abundance of incoming young within the spawning season in the Hawaiian Islands is apparent from Figure 5. The peaks of these fluctuations line up roughly with the time of new moon. This correlation is more evident from the extensive collections made from various tide pools plotted in Figure 6. The large mode of May 10 centered on a standard length of 26 mm. contains 54 transforming fish. The time of new moon was May 13. The large mode of April 17 is centered on a standard length of 27 mm. and contains 10 transforming manini. New moon in April occurred on the 13th day.

Tester and Takata (1953: 36, fig. 14) have demonstrated a similar lunar periodicity in the appearance of young aholehole (*Kuhlia sandvicensis*) in tide pools on Oahu.

If the periodicity in the influx of manini acronuri is a function of some lunar effect on the young and not on the spawning adults, then the peak fluctuations of incoming acronuri in areas of different temperature, and hence different rates of development (see development section), should still correlate with the time of new moon. A sample of 108 small manini collected with rotenone by the author from tide pools at Onotoa Atoll, Gilbert Islands, on August 21, 1951 (Fig. 7), demonstrates that this is not the case. Onotoa is located in the central Pacific (1° 47′ S., 175° 32′ E.); the monthly mean sea surface temperatures vary only slightly from 82.5° F. (28.6° C.) throughout the year. Full moon occurred on August 16 (new moon on August 2). The large mode of Figure 7 centered on about 23 mm. standard length includes only 9 transforming specimens which average 23.5 mm. in standard length. Thus the peak influx of the fish comprising this mode is estimated at 4 or 5 days prior to August 21. This large Onotoa sample, therefore, is about 11 days out of phase with the lunar cycle of incoming young on Oahu (where the mean monthly sea surface temperatures vary from 75° to 76.5° F., or 23.9°–24.5° C., from January to April).

In order to obtain direct evidence of lunar spawning by adult manini and to more sharply delimit the spawning season, the entire catch of two trap fishermen was examined for ripe fish on 62 days from June 19, 1953, to September 3, 1954. The catch was usually brought to port alive. The fishermen would not permit the open-

ing of the body cavity without purchasing the fish, but they allowed pressure to be applied to the abdomen of each manini.

When running ripe males (the sperm of which were motile) were discovered in samples taken throughout the year, it was realized that the limits of the spawning season could not be defined by the development of the male gonad. As would be expected from Table 5, however, there were more ripe males during the spawning season than outside of it. Of 745 adult manini (since trap caught, an estimated two-thirds were

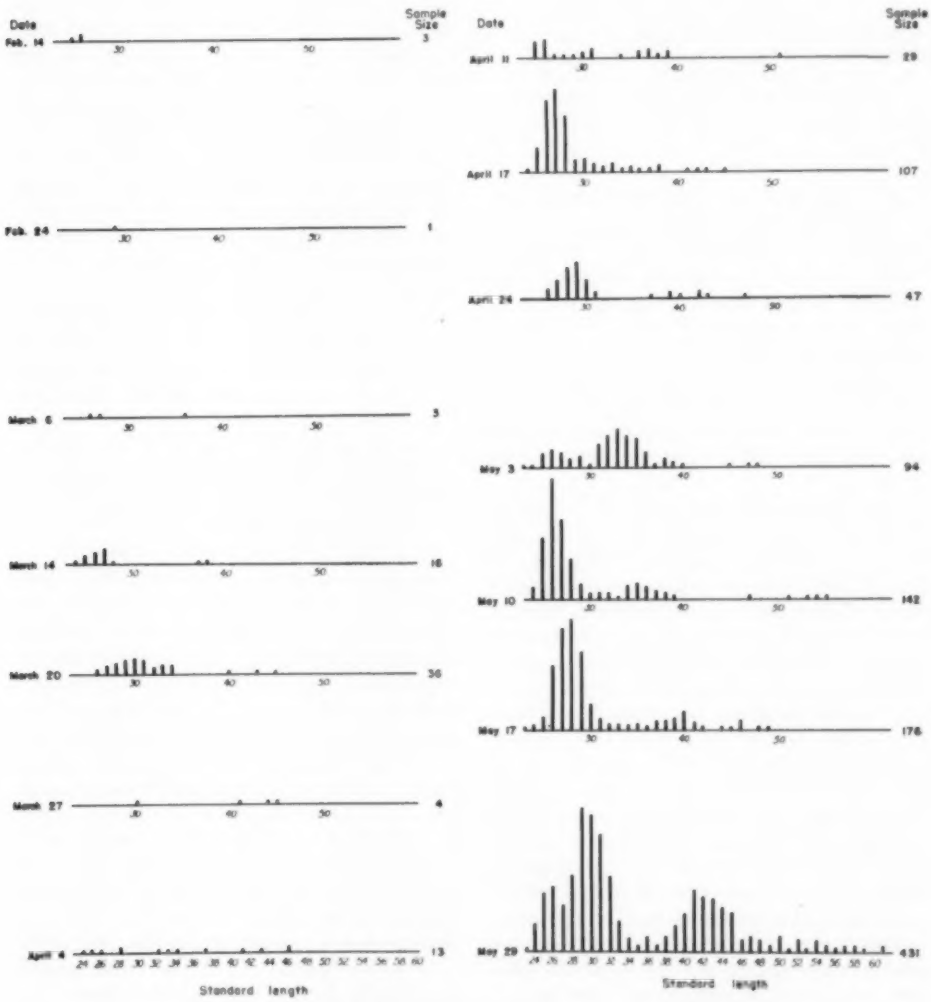

FIG. 6. Tide-pool collections of *Acanthurus triostegus sandvicensis* from Ala Wai Yacht Basin to Makapuu Point, Oahu, 1953. Vertical distance between horizontal lines is proportional to number of days between samples.

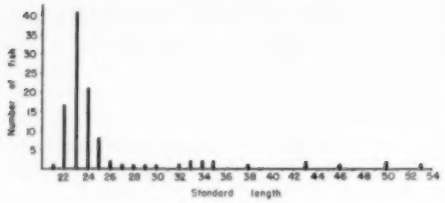

FIG. 7. Collection of *Acanthurus triostegus triostegus* from tide pools of the outer reef flat, Onotoa Atoll, Gilbert Islands, August 21, 1951. Sample size, 108. Nine specimens 21–25 mm. in standard length are transforming from the acronurus to the juvenile stage; the rest are juveniles. Time of full moon, Aug. 16.

males) examined from September to November, 11.8 per cent were running ripe males; 23 per cent of 2,419 adult manini (an estimated two-thirds of which were males) examined from February to June were running ripe males. No variation in degree of ripeness was apparent within the period of a single month. It should be emphasized, however, that no sharp dividing line exists between the condition of a running ripe male and one that is not quite running ripe, and these data tend to be subjective in this regard.

Ripe females are more easily distinguished. Fertilizable eggs of female manini are about 0.7 mm. in diameter, prefectly transparent, and are released when the abdomen is only slightly squeezed. The data on ripe females in terms of the lunar month are summarized in Table 6. As may be seen in this table, the number of fish examined on the different days ranged from 9 to 252. This variability is entirely due to variation in the catches. Also there is no regular sequence in time when the catches were examined. Scheduled sampling was not possible largely because of the great dependence of trap fishing on hydrographic conditions. In addition to being impeded by rough seas, trap fishermen are restricted by turbid water (traps are not found by surface markers but by observing through a glass-bottom box). Although the fishermen ordinarily tend their traps twice a week, they may be held in port several weeks by dirty water. A successful sampling day was also contingent on being at Kewalo Basin when the catches were unloaded. Frequently the fishermen came in unexpectedly early and their fish were promptly taken to market. Market fish were not sampled because catches of previous days may accumulate and the date when fish are caught is usually not available.

A total of 43 running ripe females were found. Thirty-nine of these were taken from 12 days before to 2 days after the full moon and only 4 from the remaining half of the lunar month. A total of 2,552 adult manini were examined in the former period, however, and only 1,311 in the latter; therefore a correction is necessary for this discrepancy in sample size. A corrected figure of 7.8 ripe females instead of 4 is the proper number to compare with 39. Nevertheless, it still remains obvious that a significantly greater number of ripe females, and hence probably greater spawning, occurs before and shortly after full moon than before and shortly after new moon. Since at least a few acronuri of all sizes (see section on transformation) enter tide pools at all times during the month and not totally in one portion thereof, some spawning might be expected throughout the month.

One sample of adult manini was examined on July 29, 1955. There were 7 running ripe female fish among the 57 manini comprising the sample. Full moon occurred on August 3.

It is not known whether spawning by the same fish takes place every month. There is evidence, however, that individual fish spawn more than once a season. The long season in itself suggests repeated spawning. If large ripe females were found at the start and progressively smaller ones throughout the rest of the season, a long spawning season might be indicated with each individual spawning only once, but no obvious trend in size of the 43 ripe females was apparent. The first ripe female of the season, which was found December 1, measured 138 mm. in standard length. The last (July 21) was also large, 140 mm. The shortest found were 106 mm. (March 13) and 101 mm. (July 14). More convincing is the failure to see any completely spent ovaries in fish during the spawning season and the observation of spent and regressing ovaries in all of the females at the end of the season. The strongest evidence concerns the finding in ripe females of a second mode of egg size

TABLE 6

RESULTS OF SAMPLING FOR RIPE FEMALE *Acanthurus triostegus sandvicensis* DURING THE SPAWNING SEASON

DATE	DAYS TO NEAREST FULL MOON		NO. OF FISH EXAMINED	NO. OF RIPE FEMALES
	Before	After		
Jun. 19, 1953	8		40	1
21	6		9	1
Jul. 14	12		114	1
17	9		45	0
21	5		14	1
Dec. 1		11	141	1
8	12		126	1
22		2	139	0
29		9	96	0
Jan. 8, 1954	11		149	1
12	7		21	1
24		5	26	0
Feb. 5	12		30	0
9	8		30	0
12	5		41	1
Mar. 2		13	31	0
12	7		144	6
30		11	44	0
Apr. 2		13	87	0
6	12		198	0
9	9		121	0
13	5		111	0
16	2		193	7
20		2	132	6
23		5	76	0
27		9	151	0
May 1		13	88	0
6	11		83	1
11	6		226	3
14	3		149	2
18		1	18	0
21		4	204	1
25		8	159	0
28		11	103	2
Jun. 11	5		42	2
18		2	97	0
22		6	29	0
25		9	49	0
Jul. 2		14	27	0
9	7		28	0
16	0	0	252	4

about half the size of the ripe egg mode, coupled with the knowledge that this mode is not retained in the ovary through the summer months. This mode of intermediate-size eggs appears to be a persistent unit within the ovary of all mature female manini during and 1–2 months before the spawning season, suggesting that it constitutes a static mass of eggs from which modes of ripe eggs may develop periodically. It is not known whether this mass is built up constantly or at short intervals from the huge reserve of minute primordial eggs which is present in the ovary of every adult female regardless of the time of year (and is here not considered as a mode of egg size).

The procedure for the determination of egg diameters was as follows: Tiny sections were snipped from various parts of an ovary (which was previously preserved in 8 per cent formaldehyde solution) and placed in water in a Syra-

cuse watch glass; the eggs were teased from the ovarian tissue with dissecting needles; the egg diameters were then measured with an ocular micrometer at × 24. Many of the eggs were oblong, probably because of unequal pressure of adjacent eggs at the time of preservation. Instead of measuring the greatest or least diameter, the eggs were moved into position by moving, but not turning, the watch glass on the micrometer image which remained fixed in a horizontal position. This method reduces the possibility of bias but has the disadvantage of increasing the spread of modal groups on graphs of egg diameter measurements.

Graphs of the egg diameters of ovaries from 9 adult female manini are shown in Figure 8. These graphs do not show any definite sequence.

Graph *C*, of a 15 mm. ovary from a female taken on January 2, for example, portrays the egg diameter pattern of an immature but maturing ovary. No graphs were made of egg diameters of ovaries from adult fish taken in August because the fish have only primordial eggs about 1 to 3 micrometer units (.035 to .105 mm.) in diameter except for those in which larger eggs are being resorbed. The relative size of the group of primordial eggs was estimated only for the ovary graphically illustrated in *A*.

Except for the immature gonad of *C*, all of the ovaries display a mode of egg size centered on about 10 to 12 micrometer units in diameter. This prompted the examination of samples of eggs from 54 ovaries taken from female fish throughout the year (more, however, from mature females during the spawning season). Sufficient eggs from each ovary were measured to determine the presence of obvious modal groups. A definite mode at from 9 to 12 micrometer units in egg diameter occurred in 46 of the ovaries, 15 to 35 mm. in length, from fish caught from September 15 to July 21. The median of this mode of 38 of these fish appears to lie between 10 and 12 micrometer units. In the ovaries of 8 fish, the median lies between about 9 and 10 units. One of these fish is the only running ripe female of the 54 examined. The remaining eight fish lack an intermediate-size mode; all of these have small gonads. No specimens were found among the 54 females with a group of eggs which have an average diameter greater than 12 units but less than the 20 to 21 unit average size of ripe eggs. Also, when checking for ripe females among the 3,863 adult manini of Table 6, the eggs pressed from the body cavity of few, if any, of these were of a size between that of the usual mode and the ripe egg mode. It is expected that such a size would be extruded with moderate pressure on the abdomen of the fish, since eggs of about 10 micrometer units (0.35 mm.) are frequently forced out. Eggs as large or nearly as large as completely ripe eggs, but in which small opaque white regions were visible, were seen almost as often as the ripe, perfectly transparent eggs. These can not be fertilized, and females containing them were not considered among the ripe fish previously discussed. The failure to find a mode of eggs intermediate in size between about 10 and 20 micrometer units suggests that eggs maturing from the former modal group (the eggs of which are opaque) do so rapidly. Perhaps the enlargement is essentially a process of hydration.

In view of the finding of so few female manini with fertilizable eggs during the season, it is further believed that the ripe eggs are not retained very long in the ovary. Admittedly a change in behavior of ripe females might influence the frequency with which they enter traps (a possible cessation of feeding, however, would not seem to affect the rate of entry, for the traps, as mentioned, are unbaited). Also, confinement in the traps might affect the maturation of the eggs.

If, however, it is assumed that ripe eggs are held within a female no longer than 1 day on the average, and 43 ripe female fish is the number that would be present in truly random samples of the population equal in size to the ones taken, then the small number of ripe females actually constitutes an indication that every adult female spawns once each lunar month. Since the lunar month is 29.53 days, only about one-thirtieth of the females sampled from the population during the spawning season would be ripe. As mentioned, 3,863 adult manini were examined during the 1953–54 season, an estimated one-third of which, or 1,288, were females. One-thirtieth of 1,288 is 43, precisely the number of ripe females which were found.

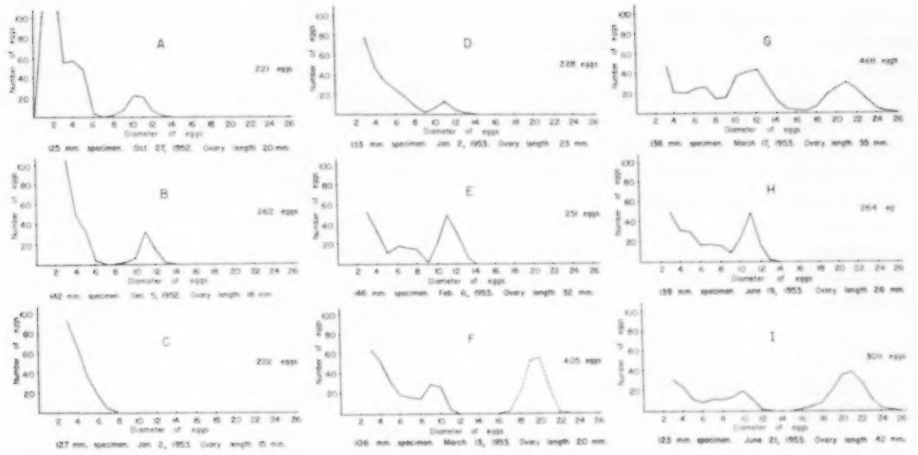

FIG. 8. Egg diameters of *Acanthurus triostegus sandvicensis* plotted as units of an ocular micrometer. Scale: 1 unit = .035 mm. Except for *A*, where the number of eggs of 1 and 2 micrometer units were estimated at 1,575 and 627, respectively, no eggs less than 3 micrometer units were measured.

Spawning

The spawning of *A. triostegus sandvicensis* was never witnessed, in spite of considerable observation both at night and during the day and at various times of the month. On June 12, 1957 (full moon) *A. triostegus triostegus* was observed to spawn at the atoll of Tikahau in the Tuamotu Archipelago at dusk (5:30 P.M.). It is believed that the failure to see the Hawaiian manini spawn was due to the lack of effort at dusk. The following account of the reproduction of the Tuamotu manini is probably similar to that for the Hawaiian subspecies.

Several hundred spawning *A. triostegus triostegus* were observed in the pass at a depth of about 25 ft. Many of the fish displayed a marked color change. The black bars on the side of the body were much broader (but the added width on either side of each bar was not as intense a black as the center); the median fins were dark, almost black, except for the middle of the caudal which remained pale; the dark median band on the forehead was prominent. Five fish of this color pattern were speared (when pursued, an individual dark-colored manini resumed normal coloration within about 10 sec.); all 5 were ripe males. As many as 4 or 5 of these more melanistic fish were repeatedly observed chasing single fish which were unchanged in color pattern. Two of the normally colored manini were speared. One was a running ripe female and the other a female with opaque eggs which were squeezed from the body only with considerable pressure; thus not all females in the spawning aggregation are capable of reproduction at the same time, which is in keeping with the finding of running ripe female manini in Hawaii along with fish with maturing ova on many different days of the lunar month (Table 6). Actual spawning took place among small groups of fish within the large school which became increasingly active and suddenly darted upward about 8 ft. above the rest. Eggs and sperm were released at the apex of this movement. Swimming was more rapid as the apex was approached. The fish dispersed as they swam back down to mingle with the school. At times two or more small groups joined together in the first few feet of the upward movement, resulting in a dozen or more fish in a compact mass at the top. The attempts to spear individual fish broke up the one large aggregation into several lesser ones in which spawning took place infrequently.

Two other surgeonfishes, *Ctenochaetus striatus* (Quoy and Gaimard) and *Zebrasoma scopas* (Cuvier), were observed to spawn in the Society Islands. Like the manini, they exhibited the sudden upward rush prior to spawning. Possibly the release of eggs and sperm is facilitated by the expansion of the airbladder from the decreasing pressure caused by the upward swimming movement. Like the manini in the pass at Tikahau, both of these surgeonfishes were spawning in a region of strong current to the open sea.

Size and Age at Maturity

The smallest running ripe female seen by me was 101 mm. in standard length. The smallest running ripe male was 97 mm. in standard length. These are probably near the minimum lengths for mature manini around Oahu.

Ten manini were reared in a large concrete tank of the Hawaii Marine Laboratory at Coconut Island from a size of 25 to 27 mm. in standard length beginning on March 17, 1953 (see detailed discussion in section on growth). Two fish of this group, an 89.5 mm. male and a 99 mm. female were killed for gonad study on July 24, 1953. The female had an immature gonad, clear gray in color, and only 5 mm. in length. The ova were minute, only 0.015 to 0.03 mm. in diameter. The male was detected because it was possible to strip a small amount of milt from it, although considerable pressure on the abdomen was necessary. The sperm, however, were not motile. Its testis was slender and 6 mm. long. Subsequent examination of the gonads of the remaining 8 captive manini was not made because of arrested growth of these fish following inadvertent destruction of the algal food supply when seining the tank.

There appears to be considerable variability in the size at maturity. This variability is apparent when the 101 mm. ripe female manini is contrasted with the 127 mm. immature specimen whose egg diameters are graphically illustrated in Figure 8, *C*.

It is doubtful that any female manini spawn during the season in which they first arrived as acronuri in tide pools. Even if the 99 mm. female, which was killed on July 24 following its growth in captivity from a small juvenile on March 17, had been among the first few arrivals to shallow water of the season (middle February), another month of growth and gonad development would hardly seem sufficient to bring a tiny immature ovary such as that seen in this specimen on July 24 to full maturity before the season ended. It also seems unlikely that males will spawn within their first season following recruitment to tide pools.

It seems probable, from a knowledge of growth (see growth section) and the approximate size at maturity, that some manini will spawn in the season following their first sojourn as juveniles in inshore waters. This would be very likely for the first young of the season; the last young of the season would not seem to have sufficient time to develop to sexual maturity before the following spawning season ended. Such a situation would probably increase the variation in the size of the fish at maturity.

Fecundity

Fecundity is defined as the total number of ripe eggs produced by a female in 1 year. It is impossible to ascertain this for fish like the manini which may spawn more than once a year, when the number of spawnings per year is unknown. Therefore only the number of eggs released at one spawning can be determined. This was attempted for only a single manini.

The fish chosen for the egg count was the 123 mm. June 21 specimen, the egg diameters of which are plotted in Figure 8, *I*. This fish had a very large ovary (42 mm. in length) which contained a high percentage of large eggs. These eggs were not completely transparent, and none appeared to have been expelled by the fish. The ovary was vigorously shaken in the vial in which it had been preserved with a minimum of fluid. The agitation released nearly all of the near-ripe eggs from ovarian tissue and placed them in uniform suspension. The contents of the vial were then placed in a graduated cylinder, allowed to settle, and the small amount of excess fluid poured off. A sample of the ovarian mass was drawn off. After its removal, the volume was computed as 26 per cent of the total. All of the large eggs in this sample were counted in successive lots placed in a Petri dish under a binocular dissecting microscope. The sample

contained 10,814 large eggs. The total number of large eggs in this ovary was therefore estimated at 40,000.

DEVELOPMENT

Fertilization of the eggs of the manini was effected artificially, using live fish obtained from trap fishermen. As previously discussed, ripe female fish are detected by the release of perfectly transparent eggs following gentle pressure on the abdomen. The milt of running ripe male manini oozes even more readily from the fish than the eggs of ripe females; however, it was found that eggs could be fertilized with sperm from males in which definite squeezing was necessary to bring forth the milt. Eggs were fertilized both by stripping ripe males and females concurrently into sea water with genital apertures in close proximity and by stripping them separately into different containers and subsequently mixing the contents.

The fertilized eggs are spherical, 0.66 to 0.70 mm. in diameter, and contain a single oil globule which is 0.165 mm. in diameter. If suspended in sea water, the eggs slowly rise to the surface. They exhibit no stickiness and do not adhere to objects or one another, although they often lie in single-layered groups at the surface.

Unfertilized (but fertile) eggs are also less dense than sea water. No difference in diameter of unfertilized and fertilized eggs could be detected.

Developing eggs were placed in large finger bowls, an aerated battery jar, and an aerated 20 gal. aquarium. In all of these containers heavy mortality of the larvae ensued because of settling to the bottom (probably through contact with bacteria there and not to any physical injury). Efforts were made to keep the larvae in suspension by placing a fine-mesh false bottom in a battery jar and locating a bubbling aerator stone beneath a hole at one side and by installing a paddle which was slowly turned by an electric motor. Although these methods reduced the amount of settling, mortality was still high and only a few larvae survived to an age of 5 days or more, when oriented swimming began.

In view of the difficulty of rearing larvae in rigid containers, a new approach was tried for the manini. A fine-mesh bag, 1.2 m. on a side, with cork along the top was floated in the Ala Wai Yacht Basin. Fertilized eggs were placed within and allowed to develop. Approximately the same mortality resulted, however.

Once the manini larvae were capable of oriented swimming, they were maintained as easily in unaerated finger bowls as any other way. At this time the critical factor became the supply of food.

The principal stages in early development from 0 hr. to 5 days 22 hr. are shown in Figures 9–12. The drawings of eggs before hatching were made shortly after placing the eggs in 10 per cent acetic acid, a treatment which makes the blastodisc opaque white and the cleavage pattern more visible. The ages given are based on an average development temperature of 24° C. During development the temperature was 24° C. ± about 1°.

Although temperature control was not sufficiently precise to permit an assay of the change of rate of development with changing temperature, it was obvious from the rearing of one batch of eggs at 26° C. ± 1°, that temperature has a marked effect on the rate. The stage attained at 28 hr. 40 min. at 24° C. was reached in about 22 hr. 30 min. at 26° C. The 42-hr. stage at 24° C. was reached in about 32 hr. at 26° C.

No attempt was made to determine the temperature limits within which normal development of the manini is possible. Due to proximity of a light bulb, the temperature of one finger bowl in which 37-hr. larvae were developing was inadvertently raised in a short time to 29.3° C. None of the larvae died at this time.

The blastodisc of the fertilized egg is 0.4 mm. long. One hour after fertilization the first cleavage becomes apparent. At the end of the second hour 8 cells are present, and after 4 hr. about 55 cells can be counted in the blastodisc.

At the age of 6 hr. gastrulation is under way. Epiboly is evident from the thin layer with a wavy edge which is extending downward over the yolk. The cells are very small and are not shown in the drawing of this and subsequent stages.

At 14 hr. the primitive streak is apparent and the cephalic region of the embryo well developed. By about 18 hr. epiboly is complete, and

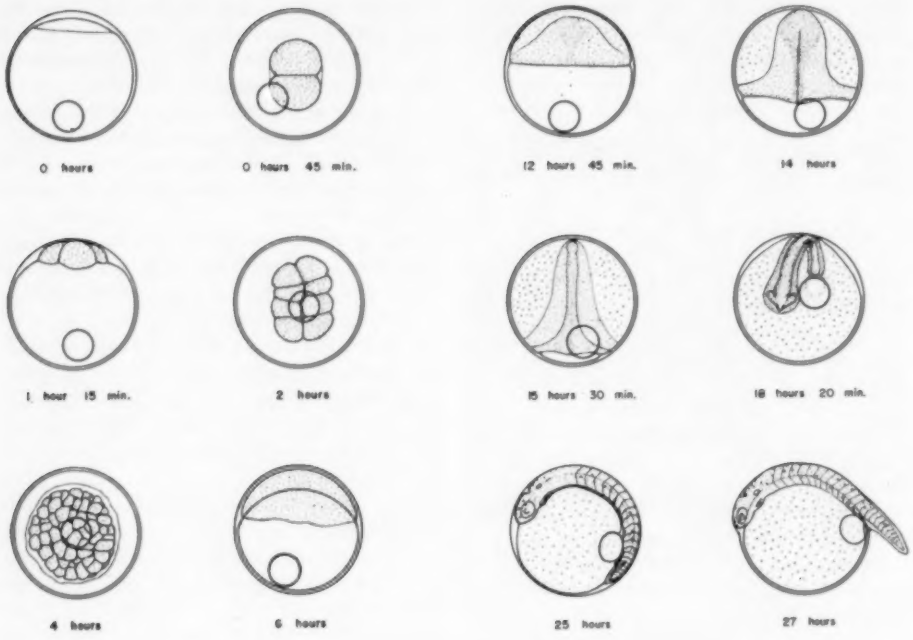

FIG. 9. Developing eggs of *Acanthurus triostegus sandvicensis*. Egg diameter, 0.67 mm.

the yolk plug is visible as a small clear area near the oil globule.

By 15 hr. 30 min. the body of the embryo is beginning to take form and elongate over the yolk. At 18 hr. 20 min. 9 somites can be counted and the optic vesicles are prominent. At 21 hr. 45 min. 12 somites are present. At 25 hr. 19 or 20 somites are visible; the lens of the eye is just starting to form; the auditory vesicle is present and the statoliths are just forming; 24 tiny melanophores can be seen in lateral view on the body; twitching movements are common; the heart contains blood although it has not yet started to beat.

Hatching occurs at the age of about 26 hr. At 27 hr. the larva is nearly 1.7 mm. in length and has 22 somites; the heart is still quiescent. At 31 hr. the heart was observed to beat; occasional short random swimming movements occur by rapid vibration of the posterior half of the body.

At the age of 42 hr. the amount of yolk is reduced to about half of what is present in the 31-hr. larva. As the yolk is used up, the larvae show a progressive tendency to sink. Larvae of 39 hr. still float head down at the surface, but 42.5-hr. fish have begun to settle. The rate of settling of 1 larva at this age was measured at 1.2 cm. per min. The average rate of 3 44.5-hr. larvae was 1.67 cm. per min., and the average rate of 4 47-hr. larvae was 1.88 cm. per min. One 71-hr. larva sank at the rate of 8.2 cm. per min.

At 42.5 hr. some larvae were already settling out at the bottom of the aquarium. Most, however, maintained their level by swimming movements. 300 such movements were observed in an aquarium which contained several hundred larvae. Of these movements, 227 resulted in the larvae being in a higher position in the tank; the rest were sideways or downward. Movements which consisted only of a twitch were not

counted. The ability to overcome settling is more efficient than 227 movements with an upward component out of 300 would indicate. Since the head is directed downward, swimming is initiated in this direction. In most cases the fish soon turn sharply and swim upward. If the interval of movement is short, there may be insufficient time to end up higher than the starting position, but usually the fish is not significantly lower. The interval between movements is highly variable, but it averages about 1 min. The distance traveled by the larvae per movement is usually less than 40 mm. One, however, stopped 110 mm. above its starting position.

In addition to geotaxic responses, swimming movements were made to avoid contact with an approaching object. This was first observed in 42-hr. larvae; however, it may be operative several hours earlier. The eyes do not seem sufficiently well developed to be functional at this early age, and a glass rod is detected as easily as an opaque one; thus vision would not seem to be the sense responsible for perception of an approaching object. Before such an object touches a larva, and sometimes when it is as far as 2 or 3 cm. away, a fleeing movement is initiated. A second stimulus soon after the flight reaction will usually result in a second swimming movement. Contact with the bottom due to slow settling usually will not result in a swimming movement. Regular movements occur at about the same rate when the fish are on the bottom. They may enable a larva to become suspended again, but usually only for a short time.

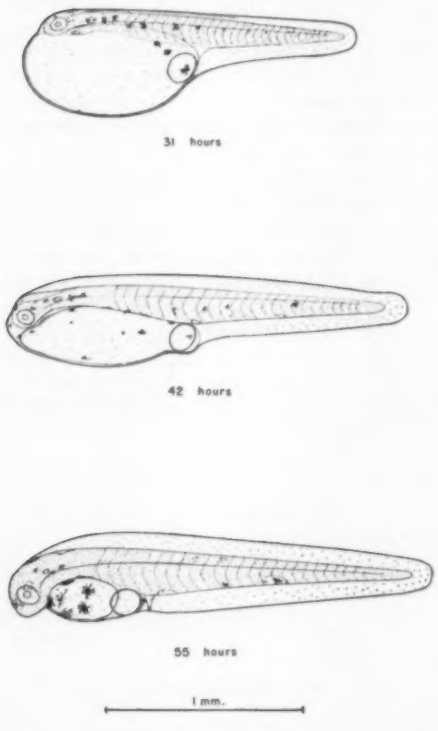

FIG. 10. Early larval stages of *Acanthurus triostegus sandvicensis*.

Areas of white pigment are beginning to form on the ventral part of the seventh and fifteenth somites of the 42-hr. larva. These are large and conspicuous in the 54-hr. larva, and lesser white areas may be seen on the ventral part of the body anterior to the seventh somite and on the head. At this stage the intestine has just formed and the yolk mass is small. The melanophores over the yolk are large and dendritic.

Figure 11 consists of microphotographs of living 75-hr. and 4-day 1-hr. larvae with the light transmitted through the little fish. The dorsal fin fold is a prominent feature at 75 hr. (it was first noticed in the 66-hr. larva), and the pectoral fins are developing. Dark pigment around the eye is evident. The 4-day 1-hr. larva was observed to sink less rapidly than prior stages. One larva of this age sank 2.5 cm. per min. and another less than 1 cm. per min. The 4-day 12-hr. larva remained suspended head down in the water, thus indicating that the air bladder was functional. The jaws were observed to move in the 4-day 5-hr. larva (Fig. 12).

Although still tending to float head downward, the 5-day larva is capable of normal oriented swimming. The pectoral fins can be fluttered rapidly, and the eyes move. The yolk is completely gone and the oil globule half resorbed. By 5 days 12 hr., the 3 individuals which survived to this age appeared to be feeding by short darting movements. Material from a culture of marine ciliates was added to the finger bowl in which these 3 larvae were kept. One

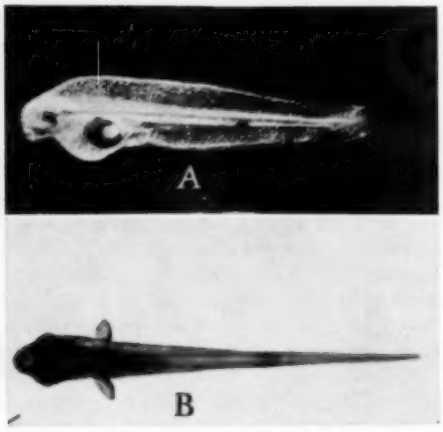

FIG. 11. Microphotographs of larval *Acanthurus triostegus sandvicensis*. *A*. Side view of 75-hr. larva; length 2.3 mm. *B*. Four-day 1-hr. larva in top view; length, 2.5 mm.

died after 5 days 17 hr. of development. Food was present in the intestine of this specimen. The second member of this trio was observed to be dying at the age of 5 days 22 hr. It was removed from the finger bowl for the lower drawing of Figure 12. As may be seen in this drawing, no trace of the oil globule remains, the intestine is convoluted, the liver is prominent, and the gall bladder is visible. The two large white areas on the body have disappeared. The total length is nearly 2.7 mm. The last larva survived to the age of 6 days 12 hr. It grew very little in the last 24 hr., presumably because of insufficient or inadequate food.

Three of the 11 acanthurid lavae from the POFI plankton collections (see p. 216) were identified as manini by dorsal and anal fin-ray counts. They are 6.6–7.0 mm. in total length. Figure 13 is a drawing of the 6.6 mm. specimen (standard length 5.3 mm.). The teeth are not visible without opening the jaws. They are simple canines. The total length of the anterior upper teeth is contained 3.7 times in the diameter of the pupil of the eye.

Specimens smaller than this one could not be identified by ray counts, for the soft rays are not fully formed. A 4.2 mm. specimen could not be positively identified at this time to genus, for only the first three dorsal spines are sufficiently developed to distinguish them from soft rays; however this specimen is about intermediate in structure to the 5-day 22-hr. larva and the 6.6 mm. larva (though is closer to the latter). Its body depth is contained 1.8 times in the total length, and the relative length of the second dorsal, second anal, and pelvic spines is about two-thirds as great as that of the 6.6 mm. larva. The caudal fin is about half formed, the urostyle extending to the posterior part of the incipient fin.

A 4.3 mm. specimen was the only acanthurid found in the POFI larval fish collections which were taken with a 6-ft. modified Isaacs-Kidd trawl, except for an 18 mm. *Zebrasoma veliferum* (Randall, 1955*c*: fig. 3). It was captured near the surface off Kahuku, Oahu. Although a little longer than the specimen just mentioned, it is in a slightly earlier stage of development and is probably a different species. If a large series of specimens were available instead of just a few it might be possible to identify the various stages of the manini to the size where fin-ray counts alone can provide definite identification.

No postlarval specimens of *Acanthurus* greater than 8.7 mm. in length but smaller than the acronurus form were found in any of the POFI collections or museum collections. As previously discussed, specimens larger than about 9 mm.

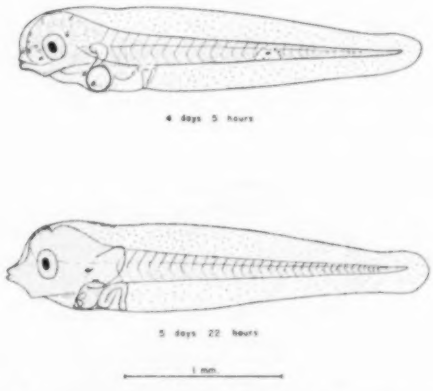

FIG. 12. Larval stages of *Acanthurus triostegus sandvicensis*.

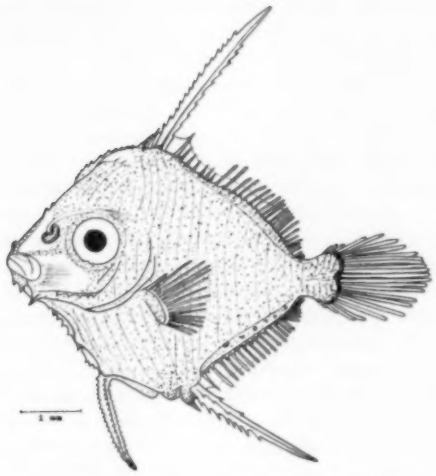

FIG. 13. Postlarval *Acanthurus triostegus sandvicensis* taken in a 1 m. plankton net at a depth of 50 m. at 22° 38′ N., 157° 11′ W.

in length probably elude a meter plankton net. The presence of the 18 mm. *Zebrasoma veliferum* in the collections from the 6-ft. trawl suggests that this would be a better means of catching larger larval acanthurids. The failure to take more acanthurids in the trawl is probably due to the great distance from land of most of the trawl tows.

The only records of the early stages of *Acanthurus* found in the literature are two postlarval *A. coeruleus* identified by Lütken (1880: pl. 5) and an unidentified 7 mm. postlarval *Acanthurus* in Weber (1913: fig. 70). Spartà (1928) reported on a long, ribbon-like, transparent, pelagic egg mass of an unknown teleost fish from the Mediterranean. The early developmental stages which he succeeded in rearing from this egg mass are remarkably similar to those of the manini. Spartà concluded that the eggs were from a species as yet unrecorded from the Mediterranean.

TRANSFORMATION

The late postlarval form of the genus *Acanthurus* is characteristic in morphology, yet identifiable to family Acanthuridae by the presence of the caudal spine and a diagnostic number of fin rays. Originally this stage was placed in a genus by itself, *Acronurus*. The name acronurus has persisted as a common name for this stage, reminiscent of the leptocephalus of eels.

Acronuri are commonly taken at night-light stations. Sixty-two manini acronuri and many of other species collected at night lights and by night-light traps offshore in the vicinity of the Hawaiian, Line, and Phoenix islands were examined. No specimens in night-light collections were found which were smaller than the acronurus stage. It is inferred, therefore, that a positive phototaxis develops in the acronurus. The lack of food material in the gut of night-light specimens (see p. 223) indicates that the presence of numerous small planktonic animals around a light at night is not the attractant. Once transformation to the juvenile stage has begun, the positive phototaxis disappears.

Figure 14 is a photograph of a live specimen of the manini acronurus taken shortly after its arrival in a tide pool. The characteristic transparent scaleless body with silvery abdomen and head (except snout and nape), disk-like form, and vertical striae on the body are apparent. The vertical bars are just beginning to form.

The acronurus comes into inshore regions

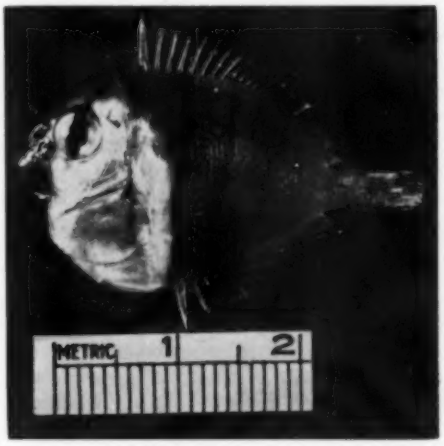

FIG. 14. The acronurus of *Acanthurus triostegus sandvicensis*. Captured at dawn in a tide pool at Diamond Head, Oahu, and photographed alive.

only at night. New arrivals to inshore areas have been collected all through the night, some as early as 9 P.M. and others just before dawn. Most of the night collecting was done at low tide. It is not known whether the influx of acronuri is greater at one phase of the tide than another.

On two occasions before midnight at low tide in ankle-deep water along the shore of the Ala Wai Yacht Basin near the entrance to the Ala Wai Canal, manini acronuri were observed just coming into the area from deeper water. They did not passively float into the shallow zone but swam in rapidly. One crossed several times through the beam of a head lamp before it was caught. If it is assumed that these fish were in deep water beyond the breaker zone before nightfall, then they must have actively swum into the harbor area and not been carried in by any tidal currents. Prior to low tide, tidal currents would be flowing out of the yacht basin and not into it. This is contrary to the belief of Breder (1949*a*: 296) that acronuri of *Acanthurus hepatus* (= *A. chirurgus*) are carried into shallow water by "vagaries of current."

Breder reported observing transforming specimens of *A. chirurgus* at sizes from 23 to 29 mm., and found juveniles from 10 to 20 mm. in length in tide pools at Bimini. He inferred that late postlarval surgeonfish reach a certain size in the plankton at which transformation is possible but continue to grow. The size at transformation is dependent on the size of the acronurus when it reaches shallow water. Breder's explanation of the cause of this variability in transformation size is plausible, although a range of at least 10 to 29 mm. for one species seems high.

From April 11 to October 4, 1953, a total of 175 manini were found in shallow water on Oahu in their first day of transformation to the juvenile stage. Their standard lengths (measured to nearest 0.5 mm.) ranged from 22 to 29.5 mm. Even this would seem, a priori, to be more variation in length than would be expected from mere growth variation alone in the pelagic habitat. A small amount of this variability in Hawaii is due to the change in temperature at which development occurs during the season (Fig. 16 and discussion below), but considerable variation can be seen in the transformation size of acronuri taken within the period of a single month, and therefore cannot be attributed to seasonal temperature differences.

The fluctuation in abundance of incoming young manini has provided an opportunity to test Breder's hypothesis. If the variation in size at transformation were entirely due to normal variation in growth, then no difference should be apparent in the size of manini which are transforming during the time of the month when a big influx is occurring and the period when the recruitment to inshore areas is minimal. If, however, more extremes in size were found when the recruitment is at a minimum, it could be assumed that growth of the manini occurs in the plankton after transformation is possible and that members of a modal group which arrive inshore and transform earlier or later than the majority of the group will be smaller and larger, respectively.

In Figure 15 the lengths of the 116 transforming manini which were collected within the period 5 days before to 5 days after peak tide-pool recruitment (taken as 2 days before the time of new moon; see p. 234 and Fig. 6) are compared to the lengths of the remaining manini caught outside this period. Clearly, a higher percentage of extremes in length at transformation occur during the part of the month when the number of acronuri entering shallow water to transform is low.

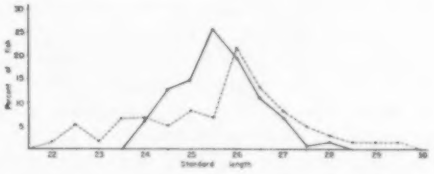

FIG. 15. Size of *Acanthurus triostegus sandvicensis* during the first day of transformation from the acronurus to the juvenile stage. The solid line represents the percent of fish at the designated standard lengths from samples taken 5 days before to 5 days after peak tide pool recruitment (3 days before new moon). The dotted line represents the percent of fish from samples taken during the rest of the lunar month. The solid line is based on a total of 116 fish and the dotted line on 59 fish. Samples include all of the first day transforming manini which were collected from Apr. 11 to Oct. 4, 1953.

If spawning of the manini occurred only during a definite small segment of the month, the dotted curve of Figure 15 would probably be bimodal, one of the modes centered on a low and the other on a high standard length. Since, however, spawning appears to occur throughout the month and merely more prominently in one part than another, most of the young resulting from fertilization at a time of low spawning intensity will come into shoal areas at a more nearly average size during the interval between periods of high tide-pool recruitment and obscure the postulated bimodal effect. The extremes in size of this small group would enter the tide-pool zone at the time of peak recruitment; thus, if the samples were large enough, both curves would extend to the same limits.

The maintenance of populations of manini around small islands such as Johnston Island, the shores of which are constantly swept by a strong current in one direction, would seem to demand some means on the part of the developing pelagic larvae to remain close to land. The presence of small eddy systems around an island might afford the explanation, provided the larvae can stay within such systems. The apparent differentiation of the manini at Johnston Island (Randall, 1956*b*: table 2) and also of *Ctenochaetus strigosus* (Randall, 1955*d*) would seem to rule out the possibility that the Johnston Island populations are derived primarily from fishes which spawn in the Hawaiian Islands proper.

While examining museum specimens of transforming manini from many localities, a definite variation in size with locality was noticed. The standard lengths of the available early transforming museum specimens were measured. These lengths (except those of Hawaiian Islands specimens, already presented graphically) are given in Table 7 with localities and with collection dates when known.

A correlation exists between the size of manini at transformation and the temperature of the water of the locality. The warmest region listed in the table is the East Indies where the mean monthly sea surface temperature may reach 85° F. (29.4° C.) (Hydrographic Office, 225). Here we find the smallest size at transformation, 20–21 mm. Small standard lengths, averaging less than 23.5 mm., are found in other warm areas such as the Palau, Marianas, Gilbert, and Marshall islands (all regions where the mean monthly sea surface temperature exceeds 81° F., or 27.3° C., during the entire year), and southern India in January, and Okinawa in September. Transforming specimens from regions where the temperature is 80° F. (26.6° C.) or less throughout the year or during the month of the date of collection are large, 24 mm. or greater in standard length. These areas include Durban (S. Africa), New South Wales, Ningpo (China), Hawaiian Islands, Mangareva, the Marquesas Islands (in August), and Clarion Island. The large transformation size of the specimens from the Phoenix Islands, where the sea surface temperature exceeds 82° F. (27.8° C.) all year, is an obvious exception to the above. Perhaps the manini population in these islands has differentiated in this respect, although the Phoenix group is not markedly isolated.

In order to preclude the possibility that the different transformation sizes of the different areas are entirely due to genetic factors (reflecting possible races of the manini in all these areas) a comparison was made of the size at transformation of specimens obtained at Oahu in an early cool and a late warm part of the season. Thirty-nine first-day transforming manini were obtained in collections from April 11 to May 8, 1953. The standard lengths of these specimens are plotted as the solid line of Figure 16. The dotted line enclosing the stippled portion of the graph represents the lengths of 38 first-day transforming manini taken from July 7 to October 4, 1953. The average sea surface temperature at Oahu from February to May is 75.7° F. (24.2° C.); the average from July to October is 79.1° F. (26.2° C.), based on average temperatures from 1941 to 1947 presented by Leipper and Anderson (1950). The mean length of the April–May group is 26.256 mm.; the mean length of the July–October group is 25.447 mm. Although the difference in length appears highly significant, a t test was made by the group comparison method (Snedecor, 1948: 80). The resulting t value of 3.11 gives a probability of nearly 0.001 of obtaining a value greater than this; thus it is extremely unlikely that samples as diverse as the above could be

TABLE 7

SIZE OF *Acanthurus triostegus* AT TRANSFORMATION FROM THE POSTLARVAL TO THE JUVENILE STATE

LOCALITY	DATE	NO. SPECIMENS	STANDARD LENGTH (mm.)	
			Range	Mean
Durban, S. Africa	May 8	2	23–25	24
S. India	Jan. 19	1	22.5	22.5
East Indies				
Sumatra	Dec. 19–25	1	21	21
Moluccas	——	10	19–21	20.2
New South Wales	——	3	24–25	24.3
Palau Is.	Aug. 3–6	7	21–23	22.1
Philippine Is.	Jun.	1	23.5	23.5
Okinawa	Sep. 6–8	2	22	22
S. Japan (30.4° N.)	——	2	21–23	22
Ningpo, China (29.5° N.)	——	5	24–26	24.9
Mariana Is.				
Guam	Jun. 28	3	22–24	22.7
	Jul. 24	7	20.5–23	21.8
	Nov. 25	2	21.5–23	21.25
Saipan	Jul. 9–14	1	22	22
Rota	Nov. 11–13	16	21.5–24	22.5
Marshall Is.				
Bikini	Apr. 1	1	23.5	23.5
	Aug. 17–18	2	22–22.5	22.25
Eniwetok	May 20	2	23–23.5	23.25
Kwajalein	Jun. 24	7	22–24	22.7
	Sep. 1	3	22–24	22
Onotoa, Gilbert Is.	Aug. 21	9	21–25	23.2
Samoa Is.				
Tutuila	Jun. 3	1	22	22
Rose	Jun. 11–14	1	24	24
Swains	May 3–9	1	25	25
Phoenix Is.				
Canton	Apr. 15–28	3	25–26.5	25.8
	May 13	3	25–27	25.8
Enderbury	May 15–19	7	25–27	25.3
Hull	Jul. 7–17	9	23–25.5	24.1
Howland I.	Sep. 24	8	23.5–26	24.3
Line Is.				
Palmyra	Jan. 18	1	23.5	23.5
Fanning	Aug.	1	24	24
Wake I.	Jun. 9	2	23.5–24	23.75
Marcus I.	Aug.	4	25–26.5	25.6
Marquesas Is.	Feb. 3	1	26	26
	Aug.	2	26–26.5	26.25
Makatea, Tuamotus	Feb. 13	3	23.5–25	24.3
	Mar. 15	8	23–25.5	24.4
Mangareva	Feb. 3	7	24–25	24.7
Tahiti	Feb.	1	26.5	26.5
	Apr. 28	1	23	23
	Jun. 16	11	22.5–26	24.2
	Jul. 8	2	23.5–24	23.75
	Aug. 12	4	22.5–24	23.4
	Aug. 28	5	23–25.5	24.4
	Oct. 4	3	25–27	25.7
	Dec. 30	17	22.5–26.5	24.5
Clarion I., Mexico	——	1	25	25

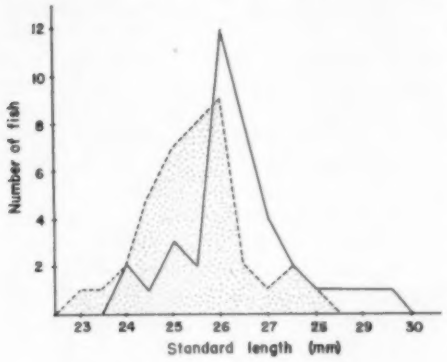

FIG. 16. Size of *Acanthurus triostegus sandvicensis* from Oahu during the first day of transformation from the acronurus to the juvenile stage. The solid line represents all of the specimens collected from Apr. 11 to May 8, 1953; the dotted line indicates those collected from Jul. 7 to Oct. 4, 1953.

drawn by chance from a population in which the transformation length was the same throughout the season. It is therefore concluded that a relationship as indicated above exists between the size of transformation of the manini and the temperature of the water.

Breder (1949*a*) stated that the complete transformation of *Acanthurus chirurgus* occurred in a period of about 48 hr. He did not, however, define the morphological state that constitutes complete transformation. In the manini, adult coloration is nearly acquired after about 48 hr., but other major changes are less than half completed after this length of time. Admittedly it is difficult to define a precise stage at which larval characteristics have completely disappeared and miniature adult structure is assumed. Probably the most convenient criterion is the stage at which the scales have completely formed. Drawings of developing scales have been made by Poey (1875: pl. 3) for the West Indian species, *Acronurus caeruleatus* (= *Acanthurus coeruleus*) and *Acronurus nigriculus* (= *Acanthurus bahianus*). The first evidence of the formation of the scales is the appearance of scattered thornlike outgrowths which project upward as well as posteriorly from the narrow, vertical, fleshy ridges of the body (these spines do not occur on the anterior half of the body). The spines are present on manini acronuri caught offshore at a night light, but they can be seen on these specimens only with the aid of a microscope. They enlarge and become visible (when wet) with the naked eye on the majority of first-day transforming individuals as early as 7:00 A.M. Each such spine on later stages was found to be a central stout ctenius of a single developing scale; the majority of scales, however, do not possess these. As scale development proceeds, the large ctenii flatten and become overlaid with epidermis. When this occurs, scale development is essentially complete as are other major changes of the transformation process. Scale development normally requires 4-5 days. In an aquarium the whole process seems delayed, and about 6 days are necessary.

Figure 17 shows transforming manini on the first, second, third, and fourth to fifth days. The second-day and third-day stages were identified with assurance by comparison with specimens recovered in tide pools following fin clipping on the first day of transformation. No older marked specimens were recovered at the stage when scale structure is just complete, and the time this required had to be inferred from the percentage of specimens in the different stages collected in the weekly poison stations of the Diamond Head tide pool of Figure 4.

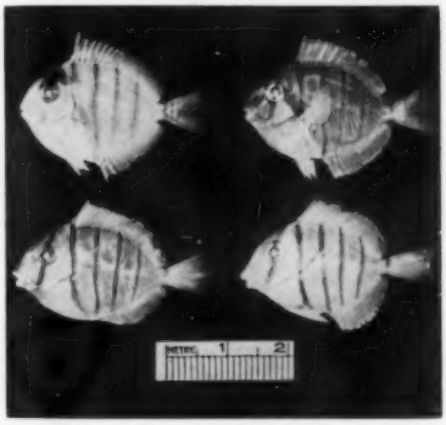

FIG. 17. Transformation of *Acanthurus triostegus sandvicensis* from the acronurus to the juvenile stage. Upper left, first day; upper right, second day; lower left, third day; lower right, fourth or fifth day.

The vertical dark bars which are so characteristic of the manini are absent from the majority of night-light specimens. They are faintly visible on a few such specimens, however. Manini caught in tide pools during the same night when they came in usually possess traces of the dark bars, but some, presumably very recent arrivals, totally lack these markings. One of the two previously mentioned specimens which were observed just entering shallow water from deeper areas of the Ala Wai Yacht Basin had traces of the bars, and the other lacked them. The bars are not dark on any of the specimens collected at night. During daylight of the first day of transformation the bars become intensely dark brown. This suggests that sunlight might accelerate or perhaps even be necessary for the darkening. In a review on the biochemistry of the production of melanin, Lerner and Fitzpatrick (1950: 119) pointed out that ultraviolet irradiation appears to be concerned with melanin formation in at least four different ways, all of which tend to increase pigmentation.

An experiment was designed to determine whether any changes occurred in the transformation process when light is excluded. Two transparent specimens which displayed no evidence of dark vertical bars on the body were taken at midnight. These were placed in a battery jar containing 2½ gal. of aerated fresh sea water. The jar was covered with a box which, in turn, was covered with a heavy black cloth. Three other transparent specimens taken at the same time were placed in a aquarium of about the same capacity which was not darkened. The battery jar was uncovered 12 hr. later. The transformation of the two specimens had barely started. The stage which was reached was about comparable to transforming fish taken shortly after dawn. The bars on the side were barely discernible and the ctenii of the developing scales on the posterior half of the body were just visible. One of the fish was on its side, dying. It was removed, and the jar was again darkened. Eight hours later the second specimen was found nearly dead. The bars were possibly a little darker; the transparency of the body was largely replaced by opaque white, an abnormal color alteration. The three aquarium specimens completed their transformation. The results suggest that light is essential to normal transformation. To be conclusive, however, the experiment should be repeated several times. If light were conclusively demonstrated to be essential to the metamorphosis of the manini, the mechanism by which it exerts its effect would still not be known. It might act directly on the tissues, or by way of the visual sense, or both.

During the first day the transparency of the body is gradually lost. By the end of the day the dark brown bars on one side of the body cannot be seen through the body from the other side as they may be on specimens such as the one in Figure 14. The bright silver color on the abdomen and head is slightly dulled by the end of the day due to the development of melanophores external to the silver layer. The iridocytes causing the silver sheen on the abdomen are present in the peritoneum. On the gill cover they occur in a layer on the underside of the opercular bones. They are found on the surface of the cleithrum at the edge of the gill opening. No silver color is present dorsal to the eye. Instead there is a broad black band which covers the brain. This is found beneath the dorsal bones of the head. By the third day both the silver color and the black band on the head are nearly imperceptible. They are, like the rest of the body except the region of the dark bars, white with numerous, close-set, small flecks of dark brown. The olivaceous cast of the body as seen on juvenile and adult manini is not conspicuous until about the fourth or fifth day of transformation, probably because of slow development of yellow chromatophores.

The second dorsal and second anal spines of the acronurus stage are longer and stouter than the other spines of these fins (Fig. 14). If stuck by either of these spines or by the pelvic spines, a stinging sensation almost comparable in intensity to a bee sting is felt. It is believed that these same spines, very elongate in the 6.6 mm. manini, are venomous in earlier stages. The poisonous nature of the spines appears to be a larval adaptation, for it is lost by the third day of transformation. A diminution in the relative length of the second dorsal and second anal spines may be seen in the series of transforming specimens of Figure 17. The relative change in length of these spines continues until, in late

juveniles and adults, the third dorsal and third anal spines are much longer than the second dorsal and second anal spines, respectively. The latter, however, remain thicker. All of the acronurus spines are T-shaped in cross-section; all are solid. The nature of the venom apparatus is unknown. The T-shape of the spines persists into the juvenile stage.

One of the most striking changes during transformation is the alteration of the configuration of the head. This consists primarily of an increase in the length of the snout, resulting in the mouth being in a more ventral position. The rostral prolongation may be seen in Figures 14 and 17. The diameter of the eye (which does not change during transformation) of the transparent specimen of Figure 14 is slightly longer than the length of the snout; in the just transformed manini the eye diameter is contained about 1.5 times in the length of the snout. The osteological changes which accompany the changes in the proportions of the head were not investigated.

A slight increase in standard length occurs during the metamorphosis to juvenile form. After 5 days in an aquarium, three transforming specimens, 24.1–25.0 mm. in standard length, increased 1.2–1.5 mm. in standard length. Most of the increase is attributable to the prolongation of the snout.

A remarkable lengthening of the digestive tract takes place during transformation (Fig. 3). In a period of 4 to 5 days the total length of the alimentary tract of the manini increases about three-fold. This lengthening occurs at the time of a change in food habits from feeding on zooplankton to feeding on algae (see pp. 222–223).

The teeth of the manini acronurus just before transformation are very different from the simple conical teeth of the postlarval manini (as seen in 6.6 to 7.0 mm. specimens). They are close-set and flattened with denticulations on the edges similar to adult teeth. There are about 14 of these teeth, each with 6 or 7 denticulations, in the upper jaw with a broad gap between teeth at the symphysis of the jaw. There are 14 such teeth in the lower jaw with 5 denticulations each. During transformation 8 large adult-type teeth (with about 12 denticulations), which are preformed within the premaxillary bone above the upper series of larval teeth, grow down over the larval teeth which are shed. The more medial of these large teeth are the largest and the first to emerge. In the lower jaw the same process occurs. Six large adult-type teeth with 7 denticulations grow over the larval teeth. Larval teeth lateral to these large ones may persist beyond the period of transformation.

The sequence of tooth replacement is not without variation from specimen to specimen. At the stage when the scales are just completely formed on the body some specimens have fewer than 8 upper and 6 lower teeth in position. Some specimens taken at night lights in deep water appear to be getting their adult teeth prematurely. One specimen of *Acanthurus triostegus triostegus* obtained at a night-light trap at anchorage at Christmas Island already had 6 large upper and 2 large lower teeth.

GROWTH

No information could be found in the literature on growth of any species of surgeonfish. The closest family, phylogenetically, to the Acanthuridae in which growth data are available for comparative purposes is the Teuthididae (Siganidae of most authors). Like the acanthurids, the teuthidids are herbivorous (Suyehiro, 1942; Al-Hussaini, 1947). Whitehouse (1923: 68–70, 83–85) reported that juveniles of *Teuthis java* grew from a length of 25 mm. in April to 75 mm. in September in Silavatturai Lagoon, Tuticorin, India. Ommanney (1949: 48–49) stated that *Siganus corallinus* (= *Teuthis corallinus*) reached a length of 180–220 mm. after 2 years' growth, and about 280 mm. at the end of the third year, in Mauritius.

Information on growth of the manini was obtained by the rearing of fish in a tank of the Hawaii Marine Laboratory, at Coconut Island, Oahu, analysis of the progression of modes among the juveniles of Figure 6, recovery of young fish marked by fin clipping, and the recovery of tagged adults. The data are discussed separately under these headings below.

The standard-length measurement for all of the work on growth of the manini is the length from the tip of the snout to the middle of the

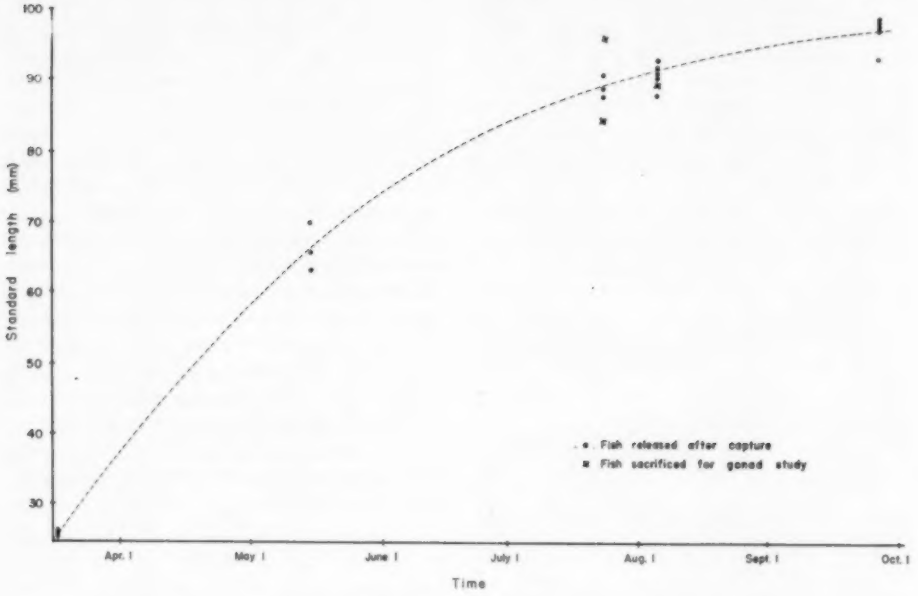

FIG. 18. Growth of *Acanthurus triostegus sandvicensis*. Based on 10 juvenile specimens, 25 to 27 mm. in length, released in a concrete tank at Coconut Island, Oahu, Mar. 17, 1953.

dorsal black bar posteriorly on the caudal peduncle. It was found that this measurement could be made with greater accuracy on living fish than the usual standard length to the base of the caudal fin (i.e., posterior edge of hypural plate). The original measurements are herein retained for all tables, graphs, and discussion (and designated simply "standard length"), rather than converting to true standard length. Should the latter measurement be desired, it may be obtained by increasing the peduncular bar length by 3.5 per cent.

Growth of Captive Fish

Ten manini, 25–27 mm. in standard length (mean length 26.4 mm.), were placed in a concrete tank at Coconut Island on March 17, 1953. The tank measures 34.7 × 10.8 ft. and is an average 3.9 ft. in depth. A constant supply of sea water is pumped into the tank. When the fish were introduced, no other fishes were present and the walls were covered with an exceedingly luxuriant growth of many species of algae. The top of the caudal fin of the 10 juveniles was removed to permanently mark them (see below) as a safeguard against the possible addition of more manini to the tank by other persons.

The growth of these fishes is recorded in Figure 18. The 3 fish captured on May 13 (mean length 66.0 mm.) had grown an average of 20 mm. per month since March 17. On August 6 all of the manini were caught (2 had disappeared and 3 were killed for gonad study). They averaged 90.9 mm. in standard length. By September 27 they had grown to an average standard length of 94.3 mm.; thus the average rate of growth from August 6 to September 27 had diminished to 1.8 mm. per month.

The manini were caught by seining the tank after partially draining it. The efforts to catch them on September 27 failed several times, and much of the algae was detached from the walls of the tank before all of the fish were netted.

Following this the amount of algae on the walls remained slight and apparently insufficient to support the growth of the fish. The 5 remaining manini were measured again on November 19. They were thin, and instead of growing they lost an average of 1.3 mm. in standard length. Manini this size shrink nearly 3 mm. in standard length when preserved in 10 per cent formaldehyde solution.

Growth Measurement from Progression of Modes

The collections of juvenile manini from Kewalo Basin to Makapuu Point, Oahu, plotted in histogram form in Figure 6 permit an estimate of the early growth rate by analysis of the progression in standard length of prominent modal groups from week to week. By this method the growth rate of juvenile manini from about 26 to 45 mm. in length is computed at about 12 mm. per month. Particular reference was made to the mode which first fully appears on the graph on April 17.

Growth of Marked Juveniles

Before undertaking the marking of juvenile manini in the field by fin clipping, experiments were performed in aquaria to test the possibility of fin regeneration. One pelvic fin and the posterior part of the soft portion of the dorsal fin were cut from 3 juvenile manini averaging 27.5 mm. in standard length. Although the fins were severed at the juncture with the body they regenerated rapidly and were nearly completely formed in a month. In a second experiment the top few rays of the caudal fin were cut away as well as the upper corner of the hypural plate to insure the removal of all fin elements. This cutting resulted in the permanent deformation of the caudal fin of the fish.

Ten manini, 28.5 to 30 mm. in standard length (mean 29.25) were caught at the Ala Wai Canal near its entrance to the Ala Wai Yacht Basin on April 24, 1953. The top of the caudal fin of these fish was removed and they were released in the same area. Three of these marked fish were recovered, 1 on May 2 which measured 32.5 mm. in standard length and 2 on May 15 which were 34.8 and 37.0 mm. long (Fig. 19). The average growth rate was 9.6 mm. per month.

Ninety-six juvenile manini, 25–28 mm. in standard length (mean 26.6 mm.), were caught, marked, and released in a Diamond Head tide pool on May 10, 1953. A total of 11 were recovered from this pool on three different dates (Fig. 19). The average growth rate of these fish was 12.9 mm. per month. The 4 manini of this group which were recovered on June 23 ranged from 42.5 mm. to 48 mm. in standard length and averaged 45.1 mm. When first caught with the 92 others on May 10, these fish were a part of the prominent mode which may be seen centered on about 26.5 mm. standard length on the graph for this date in Figure 6. This same mode is still apparent in a sample of 147 fish which were collected at Diamond Head on June 23 in an effort to recover marked fish. At this time the mode is composed of 27 fish, 40 to 49 mm. in standard length with a mean of 43.3. Since the 4 marked manini taken on this date are distributed well within the mode and of larger average size than its mean value, it is concluded that the fin clipping did not retard the growth.

The difference in growth rate between the Diamond Head marked manini and the Ala Wai marked fish may be associated with the difference in algal flora of the two areas. Algal growth in the latter area is sparse; it consists primarily of diatoms. The extraordinary growth rate of the captive manini in the Coconut Island tank is probably also associated with the nature of the algal food supply; the stand of algae was much greater than normally observed in reef or bay areas around Oahu. Invertebrates, including herbivorous types such as echinoids, gastropods, and decapod crustaceans, were present in the tank. It is assumed that the large supply of algae was primarily due to the lack of herbivorous fishes. When introduced to this unusual environment, the 10 juvenile manini were given an unprecedented opportunity for rapid growth.

In view of the more normal environment of the Diamond Head tide-pool region and the similarity in growth rate of marked fish from this region to the rate computed from the progression of modes, 12–13 mm. per month is

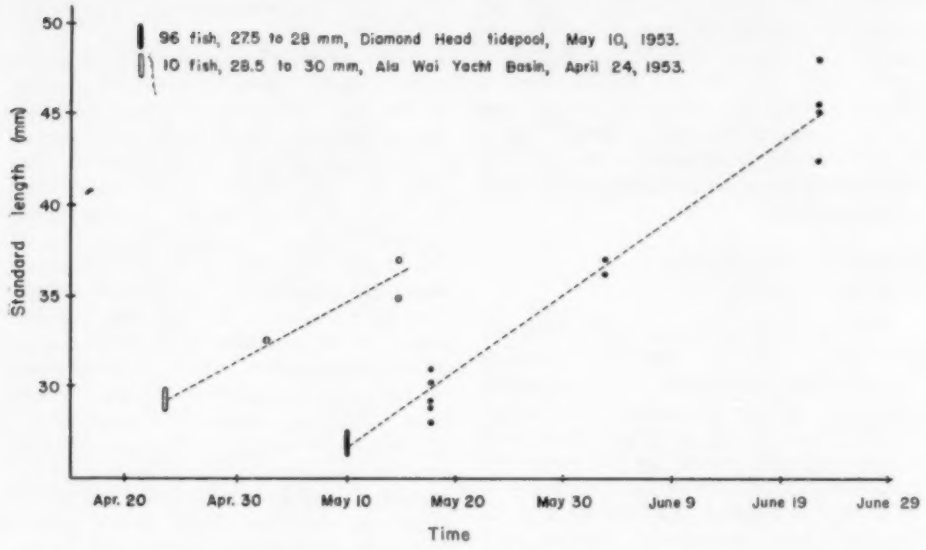

FIG. 19. Growth of juvenile *Acanthurus triostegus sandvicensis* on Oahu. Based on recovery of marked fish.

considered as the probable rate of growth in spring of early juveniles of the bulk of the Oahu manini population.

The growth of juveniles in the winter ceased. This was first noticed from shallow-water collections and observations made during the fall and winter months of 1952–53. Up to November, manini less than 40 mm. could usually be found in the collections or seen in the water. In late November, December, and January no specimens less than 40 mm. were found, but the 40 mm. size persisted. This suggests that the last incoming juveniles of the season, which enter tide pools in early October, grow to a standard length of about 40 mm. by November and then stop growing. During the next two winters the same phenomenon was noted.

In order to demonstrate this cessation of growth and to ascertain the time when growth is resumed, 22 juvenile manini, 40 to 72 mm. long, were caught with a dip net, marked by fin clipping, and released on the nights of January 5 and 6, 1954, at the entrance of the Ala Wai Canal to the Ala Wai Yacht Basin, Oahu. Fish were taken at both the northwest (Waikiki Yacht Club) and southeast shores of the canal entrance. On the two sides of the canal three basic methods of fin clipping were utilized: the top of the caudal fin was removed, the bottom of the fin, and both the top and bottom. Manini of variable size were chosen for each category, and another fin was cut on each specimen. Also any distinctive color marks (usually at the base of the pectoral fin) were noted.

Subsequent efforts to recover the fish were limited by conditions of wind, tide, and turbidity of the water. Although more subject to the effects of turbidity than exposed shores, the Ala Wai area was preferred, for fish are more restricted to the shore area because of the mud bottom away from the bank of the canal. Fish of this size in a region such as Diamond Head move well out on the reef where the broader area, deeper water, and action of surf make them difficult to capture and recapture. Although, as mentioned, some of the larger manini come into tide pools at night, their numbers are not sufficient for such a marking program.

Since fish were measured alive with a light at night, difficulty was experienced in obtaining

precise length determinations. Although the lengths were recorded to 0.5 mm., it should be added that variations as great as 1 mm. from the original measurement were noted in unbiased tests of accuracy.

Eleven of the 22 marked fish were recovered; all from the area of release. Two of these were recaptured a second time. Of the 9 fish taken before February 1, few, if any, showed significant growth (Table 8). The 4 recovered on February 21 and 27 displayed a definite increase in size, indicating a resumption of growth during this month in the area tested and for the year 1954.

One other marked fish caught in February and 2 in early March had regenerated the fin other than the caudal fin which had been cut and could not be distinguished from at least 1 other fish of their respective caudal fin categories.

Although there is some indication of a relationship between increasing water temperature and the onset of growth of these manini, the temperature data are inadequate to establish any definite correlation. Temperatures were taken in the canal at night between 9:30 and 12:00 P.M. about 3 in. beneath the surface (Table 9).

It should be emphazied that the temperature at the mouth of the Ala Wai Canal probably varies much more in a day or from day to day than the sea surface temperature off Oahu (mean water temperatures for Honolulu in 1955 are given in Hydrographic Office, 280, as follows: January 24.0; February 23.6; March 24.1). The Ala Wai area is not large and the water is therefore more subject to change due to variation in insolation and atmospheric temperature than the open sea. Probably more important are the changes produced due to variation in the run off of water from Palolo and Manoa valleys which drains to the canal and to the ever variable tides which affect this estuarine region. In order to provide adequate data for the determination of a correlation, temperatures should have been taken at regular intervals each day and an analysis of growth made in terms of average daily water temperatures.

TABLE 9

TEMPERATURE AT THE MOUTH OF THE ALA WAI CANAL

DATE	TEMP. (° C.)
Jan. 5	22.8
Jan. 20	23.2
Feb. 1	23.1
Feb. 27	25.3
Mar. 2	24.7
Mar. 21	24.9

Growth of Tagged Adults

The first tag used on the manini was the Atkins type (Rounsefell and Kask, 1945: 330, fig. 1). It consisted of a single rectangular piece of white cellulose acetate, 5 × 28 mm. in size, and was attached through the back of the fish beneath the posterior part of the dorsal fin with 4-lb. test monofilament nylon. Two small adult

TABLE 8

RECOVERY SIZE OF JUVENILES OF *Acanthurus triostegus sandvicensis* MARKED ON JANUARY 5–6, 1954

STANDARD LENGTH WHEN MARKED (mm.)	STANDARD LENGTH WHEN RECAPTURED				
	Jan. 20	Jan. 26	Feb. 1	Feb. 21	Feb. 27
40.0	41.0				
46.5	47.0				
49.0					54.5
51.5				57.0	
55.0	55.5			60.0	
55.5	55.0				
56.0		56.5			
64.0			64.0		
66.5		66.0			
70.5	70.5				
72.0	72.0			79.0	

manini were tagged and held in a tank at Coconut Island. Within 3 weeks the tags were no longer present on the fish. They were recovered from the bottom of the tank with the loops of nylon intact, thus indicating that the nylon had pulled through the flesh.

The same type of tag was then threaded through the upper part of the hypural plate of the 2 fish. As they swam, the tag of each oscillated slightly as it was drawn along in a position just above the caudal fin. Three months later both tags were in place, and the method looked auspicious. On March 3, 1953, while operating from the fishing vessel "Friendly Isle" owned by Samuel Kaolulo, 50 adult manini were tagged in this manner. Two fish were recovered 5 days later, both in the vicinity of the point of release. No other recoveries were reported. The two Coconut Island manini lost their tags before 6 months elapsed, and further plans for tagging by this method were abandoned. Disappointing results with Atkins tags have been reported by other authors, such as Fraser (1955).

Petersen disk tags were then tried. Since stainless steel seemed most promising among the metals commonly used to attach these tags (Calhoun, Fry, and Hughes, 1951), this material was chosen for initial trials. Considerable difficulty was experienced, however, in bending the free ends of the wire on a struggling fish, a disadvantage clearly pointed out by Calhoun *et al.* Attention was then shifted to nonmetallic substances, of which nylon seemed the most propitious. It is superior to metal in its pliability, nontoxicity, and in not being subject to electrolytic action or fatigue. In order to keep the disks in place, the ends were melted into knobs with a flame (Fig. 20). The position of the tag on the fish is shown in Figure 21. (For a detailed discussion of this tagging method, see Randall, 1956*a*.)

FIG. 20. Petersen disk tag used in tagging *Acanthurus triostegus sandvicensis* on Oahu. The ends of the monofilament nylon connecting the disks have been melted into knobs with a cigarette lighter. The heating caused a blackening of the one knob which is visible.

On August 6, 1953, 3 captive adult manini were tagged with plastic disks by 60-lb. test monofilament nylon (diameter, 1 mm.) and 1 with stainless steel wire.

Seven weeks after tagging, all 4 fish, along with 6 untagged fish which were measured at the time the 4 fish were tagged, were caught and remeasured. The 6 untagged fish, which had a mean standard length of 86.3 mm., had grown an average of 6.6 mm. The 3 tagged with nylon (mean standard length, 84.4 mm.) grew an average of 7.7 mm. The 93 mm. fish whose disks were attached with stainless steel wire added the smallest increment of growth, 2.5 mm. Although there are insufficient data for definite conclusions, it seems apparent that manini tagged with Petersen disk tags fastened with monofilament nylon are capable of normal growth.

One of the fish which survived 11 months until July when the tank was needed for other purposes still retained its disks fastened with nylon. It was noted that the tagging wound was small, and there was no evidence of deterioration of the nylon.

Since the experimental tagging demonstrated no obvious fault in this method, field tagging was begun. Forty-five manini were tagged with hand-made tags. This proved to be most time consuming, and assistance was requested of and granted by the Hawaii Division of Fish and Game. Manufactured tags of laminated cellulose acetate (Fig. 20) were purchased. In order to publicize the tagging, posters (Fig. 21) were

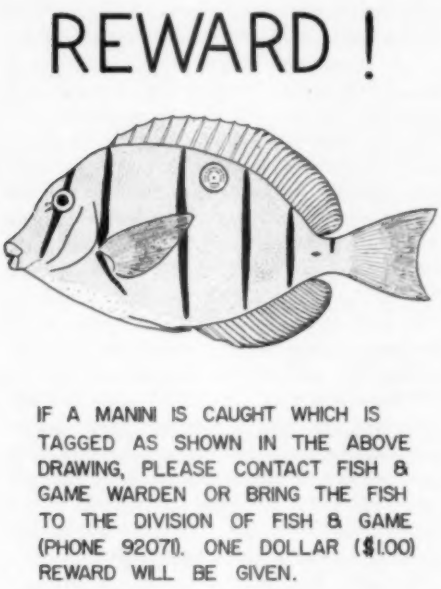
REWARD !
IF A MANINI IS CAUGHT WHICH IS TAGGED AS SHOWN IN THE ABOVE DRAWING, PLEASE CONTACT FISH & GAME WARDEN OR BRING THE FISH TO THE DIVISION OF FISH & GAME (PHONE 92071). ONE DOLLAR ($1.00) REWARD WILL BE GIVEN.

FIG. 21. Poster used to publicize tagging of *Acanthurus triostegus sandvicensis* on Oahu.

distributed by game wardens. Carl M. Nemoto, then working for the Division of Fish and Game, tagged a total of 1,157 manini, 70 to 152 mm. in standard length, from July 6 to November 23, 1954. Forty-five additional fish were tagged on May 4 and June 6, 1955. The tagging was carried out from Kaolulo's vessel between Kewalo Basin and Koko Head, Oahu. The manini were caught in traps, tagged, measured, and released at the place of capture, which was recorded.

Due to the difficulty of using a flame when tagging from a vessel exposed to the strong winds of the Kaiwi Channel (Molokai Channel), Nemoto decided to tag most of the fish by crimping brass leader sleeve on one end of the nylon (the other end was melted into a knob prior to the departure of the vessel). This method was devised by Kenji Ego of the Division of Fish and Game.

Of the total of 1,247 manini tagged with disk tags, there have been 281 recoveries. Of the recovered fish, 173 have been returned alive, providing the opportunity for re-release. Twenty-four of these have been caught again, and 3 have been taken a third time (these recoveries are included in the 281 mentioned above).

The following table shows the lapse of time by 2-week periods between the release and recovery of tagged manini.

The fish with the longest recovery time was tagged on September 21, 1954, and recovered on July 29, 1955.

The explanation of the large number of manini recovered in the first few weeks following release and the sharp drop in returns thereafter probably involves a number of factors, such as mortality, loss of tags, and movement from the immediate area of release.

It is known that at least some loss of tags has occurred, for manini with the tagging wound but without tags have been noticed by fishermen. Since no fish have been seen with a tag in the process of moving up through the back and dorsal fin, it is assumed that most of the early losses, at least, occurred from a dropping off of a disk because of the knob being too small or the brass inadequately crimped. Analysis of the returned tags indicated that the knobs were too small in many cases. When the diameter of the hole in the disk is 1 mm., the knob should measure at least 2 mm.

TABLE 10

RECOVERY TIME OF TAGGED ADULTS OF *Acanthurus triostegus sandvicensis*

WEEKS FOLLOWING RELEASE OF FISH	NO. OF FISH RECOVERED
2	96
4	57
6	42
8	25
10	17
12	9
14	6
16	5
18	4
20	4
22	3
24	5
26	2
28	2
30	2
34	1
40	1

Movement from the trap area could account for a diminution in recoveries of tagged fish; however, evidence is strong against at least extensive migration by this species (see section on migration).

The marked drop in number of recoveries still seems too high to be accounted by any or all of the above reasons. One other possibility exists which is supported by the extraordinary high percentage of early returns. A tagged manini may show a greater predilection to re-enter a trap than untagged manini to enter a first time. This phenomenon has been conclusively demonstrated by Lawrence (1952) for bluegill sunfish in Iowa farm ponds. If such a tendency exists, it might be expected to be greatest in the fish soon after release and gradually abate with time. One manini was caught, tagged, released near the next trap, and caught again in this trap a few minutes later.

The 173 tagged fish which were returned alive were measured alive a second time by Nemoto and released. The remaining tagged manini were measured after they had died, and usually not when fresh but following partial drying and/or freezing. Seventeen of the latter group were recovered within the first 2 weeks following tagging. These fish were all from 1 to 7 mm. shorter than when first measured. The average shrinkage was 3.53 mm. The average standard length of these specimens measured to the peduncular mark is 109.8 mm. The average shrinkage per millimeter of length is therefore 0.032 mm. A correction was made for each fish which was measured dead (unless freshly dead) by multiplying its recovery length by this factor and adding the product to the length.

A total of 70 tagged manini were measured alive a second time following recovery within 2 weeks of tagging. Surprisingly, 46 of these were from 1 to 5 mm. shorter than when first measured; 10 were the same size; 14 were from 1 to 3 mm. larger. The average "growth" was —1.06 mm. A t test applied to these data to ascertain the probability of obtaining such a distribution from a population in which no actual change in length occurred resulted in a t value of 5.1. With 69 degrees of freedom this gives a probability of less than 0.001 of getting a higher t value; thus the null hypothesis of no significant difference is rejected. Since the same person measured the fish both times, the reason for the significantly shorter length is not apt to be any bias in measurement. The shorter length is probably due to shrinkage from starvation in the traps. Manini which are caught in traps may have been held in the traps for a week or more. Although both measurements are made on fish caught in traps, the effects of confinement would be expected to be greater on fish spending another period in traps within 2 weeks of their first.

In order to test the hypothesis that actual shrinkage occurs during starvation, 17 trap-caught adult manini (none showed evidence of long sojourn in traps), 112 to 131 mm. in standard length, were tagged, measured, placed in two large aquaria, and allowed to starve. Eleven days later the 5 fish which survived were remeasured. A definite shrinkage of from 1 to 5 mm. (mean 3.4 mm.) had taken place. The measurements were made by Nemoto.

The large amount of variation (—5 to +3 mm.) in the series of differences between the measurements made on the 70 fish when tagged and recovered within 2 weeks was unexpected. When it is realized that five different sources contribute to this variability, it is more comprehensible. There is the possible error in the first measurement of a living fish. The second measurement of this same fish constitutes an independent source of error. The shrinkage due to starvation is a third. Some manini which are caught have not been in a trap more than a few hours and will not have shortened at all; others held prisoner for a week or more may have shrunk several millimeters. Some manini initially caught after a very short stay in a trap, tagged with a minimum of injury, and recovered a full 2 weeks later after another brief period in a trap might have grown about a millimeter; thus growth itself probably forms a fourth source. An important fifth source of error in the measurement of the dead tagged fish is the variation in shrinkage after death. All of this variability has necessitated a statistical approach to the analysis of the data, and for this purpose the large number of recoveries has been most welcome.

Only those manini recovered after spending

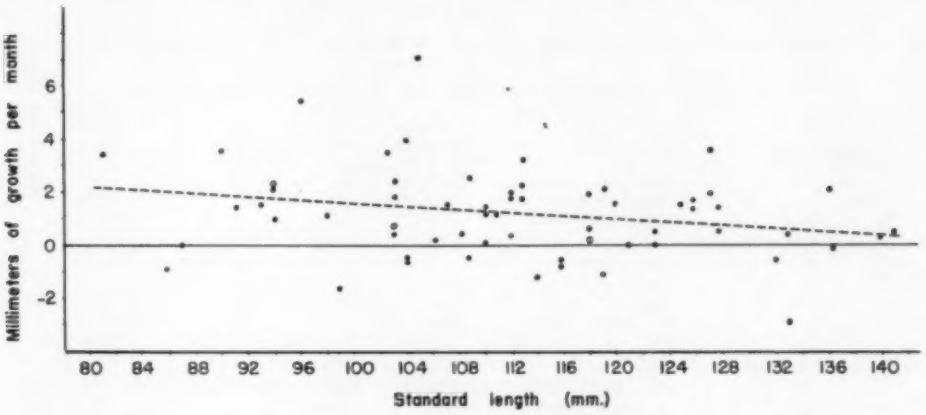

FIG. 22. Growth of *Acanthurus triostegus sandvicensis* on Oahu during the period Jul. 6 to Nov. 19, 1954. The points represent growth increment of tagged fish recovered after at least 1 month in the water. Circles indicate the superposition of one point on another. The dotted line is the regression of growth on standard length.

a month or more in the water following being tagged were utilized for growth study. In Figure 22 the data from 68 such fish, tagged between July 6, 1954, and September 28, 1954, are plotted. The dotted line represents the regression of millimeters of growth per month on standard length. The regression coefficient "b" (slope of the regression line) is —0.0292. The t value testing whether this regression differs significantly from zero is 2.085. With 66 degrees of freedom, the probability of getting a larger value of t is 0.04; thus the null hypothesis of no significant regression is rejected.

The comparison of the regression line with the upper part of the growth curve of Figure 18 is favorable. The average growth rate of the captive fish from August 6 to September 27 was given as 1.8 mm. per month. The average rate for this size range (90.0 to 94.3 mm.) from the regression line is 1.74 mm. per month.

In order to further confirm the finding of cessation of growth in winter, 155 manini were tagged on November 19 and November 23, 1954, by Nemoto. Twenty-five of these fish were recovered from December 23, 1954, to February 18, 1955 (see Fig. 23). Their average rate of growth is —0.112 mm. It therefore seems likely that no growth occurred during this period.

Tagged manini, recovered after a month or more in the sea, which were at liberty during winter and either fall or spring months have not yet been considered. Data from these fish are presented in Table 11.

If it is assumed that these 22 fish did not grow during any part or all of the 3-month period beginning November 19, and the growth rate of each is computed only from remaining months, an average growth rate of 1.8 mm. per month is obtained. This compares favorably with the rate of growth as indicated in Figure 22 (the average standard length in Table 11 is 110.6 mm.).

AGE

In view of the lack of winter growth of the manini it was hoped that annuli might be detected on the scales; however, none could be seen. Even the circuli of the tiny scales of this species are not very distinct. Cross-sections of vertebrae and otoliths were also examined, but with negative results. It was necessary to grind otoliths to about 1 mm. thickness and view them with subdued light under a compound microscope before any concentric rings could be seen. These were numerous and variable, and none were more sharply defined or grouped closer together than others.

TABLE 11

GROWTH OF *Acanthurus triostegus sandvicensis* RECOVERED AFTER 1 MONTH OR MORE FOLLOWING TAGGING

(Period of tag retention includes both winter and fall or spring months, 1954–55)

DATE RELEASED	DATE OF RECOVERY	STANDARD LENGTH	MEASURED DEAD	GROWTH (mm.)
Jul. 6	Dec. 14	105	×	3.4
23	Mar. 25	110		3.5
30	Dec. 23	115.5		5.5
Aug. 10	Feb. 6	113	×	7.8
10	Feb. 22	110		3.0
13	Jan. 28	98	×	3.1
27	May 17	97		8.0
Sep. 3	Feb. 6	101	×	7.2
3	Mar. 25	102		3.0
21	Jan. 24	98.5		4.0
21	Feb. 18	123	×	7.0
21	Feb. 21	105	×	7.4
21	Jul. 29	101		4.0
28	Dec. 23	121	×	1.8
28	Jan. 21	114		2.0
28	Mar. 25	122	×	1.8
28	Apr. 23	124		1.0
Nov. 19	Mar. 1	105	×	3.8
19	Apr. 5	152		1.5
23	Mar. 19	119		0.5
23	Apr. 27	105		3.0
23	Jul. 6	106.5		7.5

The next approach to obtaining the age of manini was the preparation of the length frequency curve of Figure 24. As the recruitment of the manini is seasonal, it seemed possible that year classes might stand out as modes on such a graph. At least for this curve, however, no definite modes are apparent. Probably the long period of recruitment (February to October), coupled with individual variation in growth, precludes the formation of distinct modal groups in standard length.

Age determinations of the manini would therefore seem possible only by rearing of fish, recovery of tagged fish (tagged at a size small enough to predict the age from growth rate with reasonable accuracy), or gross estimates from growth rate and knowledge of the maximum size.

Although the age attained by the manini is unknown, the following information on the age of two surgeonfishes supplied by Spencer Tinker, director of the Waikiki Aquarium, indicates that at least some acanthurids are long-lived. Two unicorn fish (*Naso unicornis*) which were present in the aquarium when an employee arrived in 1935, lived until they succumbed as the result of an accident in 1955. In 1940 several specimens of *Acanthurus xanthopterus* approximately 5–6 in. in length were placed in the aquarium. Two of these survived until 1951 in a small tank together; they had reached a size of about 20 in. At this time one slashed the

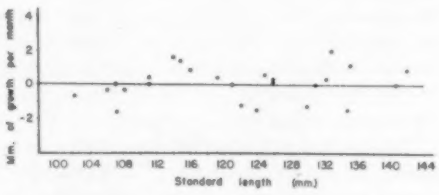

FIG. 23. Growth of *Acanthurus triostegus sandvicensis* on Oahu during the period Nov. 19, 1954, to Feb. 18, 1955, as based on the recovery of tagged fish which were in the water 1 month or more. The horizontal line was added at the zero point to facilitate comparison of the distribution of points with Figure 22.

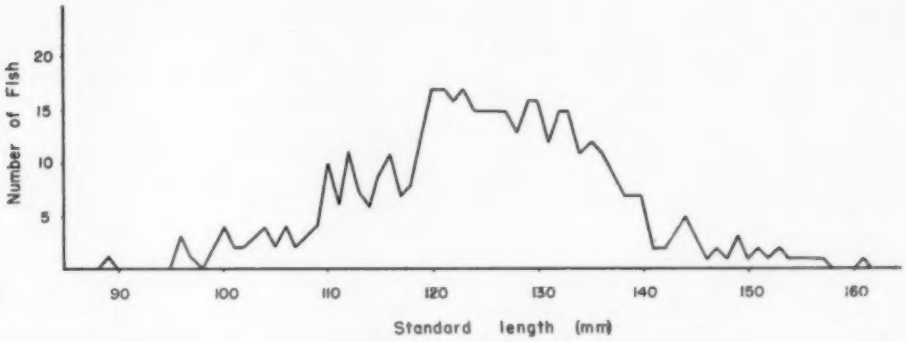

FIG. 24. Length frequency distribution of *Acanthurus triostegus sandvicensis*. Based on 426 specimens caught in traps from Kewalo Basin to Koko Head, Oahu, from Apr. 2 to 9, 1954.

other with its caudal spine and the latter ultimately died. The remaining fish died in 1955 because of an accident.

BEHAVIOR

Migration

Small juvenile manini tend to remain in the tide pool or shallow water area to which they first come from the pelagic state. Some evidence for this has already been presented. Of 176 juveniles taken in the weekly collections during a season from the tide pool of Figure 4, only 19 were 30 mm. or more in standard length and hence definite migrants to the pool from other areas. Since all of the fish in this pool were killed with rotenone each week, a much greater movement to such a large unoccupied area would be expected from the smaller adjacent pools if the species did not exhibit a tendency to remain in one location. When the adjacent pools were sampled for manini, they invariably contained many more specimens 30 mm. or larger, than less than 30 mm. It should be emphasized that these pools are isolated from one another for only about an hour or less during the infrequent low tides less than 0.0 ft. Even in areas like the shore of the Ala Wai Canal and the Ala Wai Yacht Basin where adjacent areas are freely available at all times and essentially identical in cover and food supply, appreciable movement does not take place. This is attested by the success in recovery of marked fish at the mouth of the Ala Wai Canal (Fig. 19, Table 8). Failure to take more of these fish was not due to their movement out of the area but to the difficulty in catching them. Less than one-fourth of the manini sighted were caught, and probably many others were hidden from view under large rocks, etc. None of the fish were taken farther than 20 ft. from the point of release, although the shore was searched as much as 100 ft. away.

On March 7, 1953, a juvenile manini, estimated 36 mm. in standard length, was seen next to the sea wall of the Ala Wai Yacht Basin beside a pier. It was probably among the first manini of the season to come into the area, and was the only individual this size visible for over 100 ft. of sea wall on either side of the pier. On the 9 different days up to March 28 when attempts were made to find this fish, it was seen. Its greatest movement from the place where first observed was only 12 ft. On March 28 it was caught (measured as 41 mm.), and the posterior part of the soft portion of the dorsal fin removed in order to identify it with greater certainty in further observations. It was found on 10 different days up to May 2, but never more than 12 ft. to either side of the pier. On April 24 the dorsal fin had almost completely regenerated and by May 2 the fin appeared normal.

As juvenile manini grow, they migrate seaward from the tide-pool zone (in the harbor area, as mentioned, the larger fish remain in shallow water because of the lack of cover and

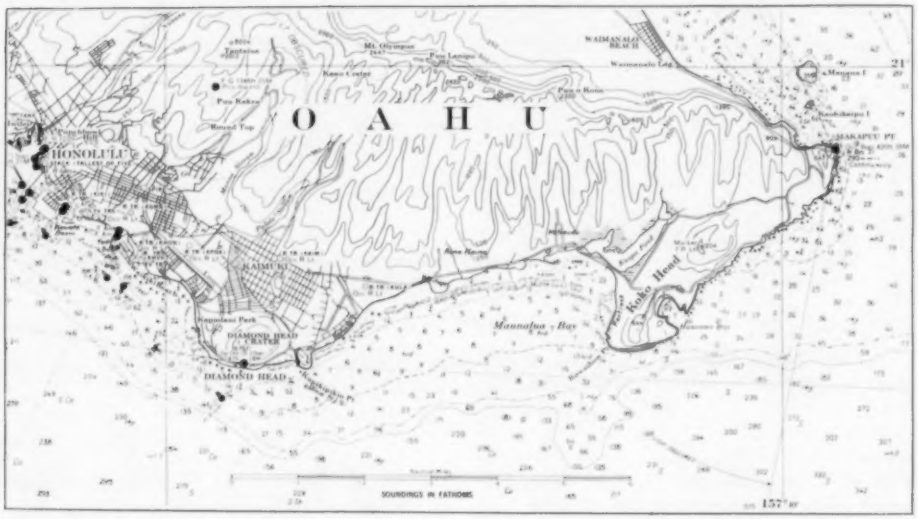

FIG. 25. Southeastern coast of Oahu, Hawaiian Islands (after U. S. Coast and Geodetic Survey Chart No. 4110).

the lack of algae on the mud bottom away from shore). This movement is demonstrated in the graphs of Figure 6. The relative size of any one modal group is progressively smaller in subsequent collections (predation would have to be extremely heavy to achieve the same diminution). The one seeming exception is the large collection of May 29. This, however, was made from a very large pool at Diamond Head which averages about 4 ft. in depth. A higher percentage of larger manini were expected from this collection than previous collections which were all made in pools less than 2 ft. deep.

Information on movements of adult manini was obtained from the recovery of tagged fish. Unfortunately, exact locality data for the areas of release and recovery were usually not available. Since Nemoto was operating from a commercial vessel solely by virtue of the kindness of Kaolulo, he could not delay the fishing to take bearings or soundings. Most locality data from fishermen who recovered tagged manini were also very nonspecific. As a result, little is known of local movements of adults, and only migrations from one major area to the next or the lack of such migrations could be ascertained.

Kaolulo's traps are arranged in groups, most of which are well separated. Nemoto designated these areas as offshore from the following: Yacht Basin, Royal Hawaiian Hotel (Waikiki), Natatorium (near Kapiolani Park), Diamond Head, Black Point, Kahala, KULA antenna, Wailupe, Aina Haina, Kuliouou, Niu Peninsula, Portlock, and Koko Head (Fig. 25).

Of the 281 recoveries of tagged manini 237 were made by Kaolulo; 126 tagged fish, most of which were early recoveries by Kaolulo, were returned to the Division of Fish and Game with no record of where they were caught. This difficulty arose because of his resorting to memory alone to recall the area where tagged fish were taken. When he caught several fish he usually admitted that he could not be sure where any of them were caught. He was finally persuaded to keep record of locality by tag number.

One hundred and thirty-two tagged manini were recovered which exhibited no definite migration. Ignoring fish released in Kewalo Basin for the moment, this leaves only 11 records which indicate that some migration might have occurred. Five of these were fish which were displaced from their home area by movement of

the vessel to the next area and which apparently returned to the home area. One was caught at Wailupe, released at Black Point, and caught again at Wailupe. The same fish was not released the second time until the Kuliouou area was entered. It was caught a third time back at Wailupe. Another Wailupe manini was released opposite the KULA antenna and was recovered at Wailupe. Two fish were caught at Black Point, released farther offshore at Kahala, and caught again at Black Point. The remaining 6 records are as follows: 1 fish supposedly migrated from Kuliouou to Wailupe; another went from the KULA antenna to Niu Valley; 2 apparently went from Kuliouou to Wailupe; the last 2 swam from Black Point to Kuliouou. The possibility of error must be kept foremost in mind for all of these apparent migrations. The 2 manini which moved from Black Point to Kuliouou were both caught by Kaolulo on the same day, which seems unusual.

In view of the manner in which the locality data have been reported, it is surprising that more alleged migrations have not taken place. It is therefore concluded that extensive migrations of this surgeonfish probably do not normally occur.

Of the 172 tagged manini which were released a second time 125 were set free on Kewalo Basin. Twelve of these have been recovered. One was taken between piers 7 and 8 in Honolulu Harbor. The rest were all captured either at Kewalo or in the Diamond Head direction. One was taken from a tuna boat in the basin, and 2 off the Kewalo breakwater. One locality reads Ala Moana and another Ala Wai. One manini was caught by Kaolulo with no record of locality. Since his nearest trap is off the Yacht Basin, this fish must have migrated at least this far. One manini released at Kewalo was caught at a depth of 30 ft. directly off the Royal Hawaiian Hotel. A fish from Black Point was caught 6 months later at wading depth off Diamond Head not far from Black Point. The most interesting recoveries of Kewalo-released fish are 2 from Kuliouou which were originally captured at Kuliouou and 1 at Wailupe which was first caught off Wailupe. Although, again, the possibility of error must be kept in mind, it seems unlikely that the only 3 examples of extensive migration (about 8 mi.), all of which occurred among the 12 fish recovered following release at Kewalo Basin, could be mistakes. One of the Kuliouou manini was recorded from this area by tag number by Kaolulo. When questioned of any chance of error, he insisted there could be no mistake. An interval of 3½ months elapsed between its release in Kewalo and its final capture. The other Kuliouou fish was obtained from the Young Market in Honolulu. The interval between the release and capture of this fish was 16 days. The Wailupe fish was recovered by Kaolulo 1 month after release in Kewalo Basin. The locality was reported verbally. The intriguing interpretation of these 3 records of long migration is that at least some manini removed from their home area will continue to wander on the reef until they return. Three records are too few on which to base such a conclusion; therefore more data should be obtained by purposely displacing tagged manini considerable distances from the original area of capture.

Aggregations

Adult manini are often observed in large feeding aggregations which slowly move over the bottom. These groups of fish may be dense and cover areas more than 50 ft. in diameter. What appears to be the same school was repeatedly seen in the same general location at the northwestern end of Manana Island. This group of fish was observed in the area in fall as well as during the breeding season. The behavior of individual manini of the school did not seem to differ from that of solitary adults.

One school of about 300 adult *Acanthurus triostegus triostegus* was observed in the northeast side of the pass at Takaroa, Tuamotu Archipelago, over a period of a week. The school moved as a close-knit mass several feet off the bottom, stopping frequently for periods of several minutes to graze algae. One or two *Aulostomus chinensis* were observed to accompany the school, and the manini were almost constantly harassed by *Acanthurus glaucopareius* which chased individual fish. The school moved as much as 300 yd. in several hours.

Juvenile manini are gregarious and are often seen swimming in groups. One group of 11 individuals, all less than about 36 mm. in standard

length, was observed for a period of half an hour at the shore of the Ala Wai Yacht Basin. No fish became separated by more than 12 in. from the rest of the group.

The schooling of *A. triostegus triostegus* during spawning has been discussed previously.

Reaction to Danger

Juvenile manini along the shore of a part of the Ala Wai Canal infrequently visited by man perceive the approach of a person walking along the bank from an average distance of about 20 ft. This distance is contingent on the position of the sun and the depth and turbidity of the water. The usual reaction is a swift darting to some immediate hiding place. If an observer remains immobile, the fish come out of hiding in from about 15 to 25 sec. and resume feeding shortly thereafter. Manini of the same size next to the sea wall of the Ala Wai Yacht Basin, where people pass almost continuously, do not interrupt their feeding at the approach of a person unless some unusual sharp movement is made, at which time they may hide.

The manini in a large tide pool at Diamond Head were observed to have two hiding places, each beneath ledges at the side of the pool. One of these was preferred, and most of the fish swam to it when the pool was approached. When rotenone was spread in the region of this retreat, all of the fish swam rapidly in a direct line to the second ledge, in spite of the turbidity of the water (from the rotenone), even though they had to move in the direction of the observer and pass over a very shallow part of the pool. The part of the pool away from the observer was broader, deeper, free of rotenone at the time, but without good cover. It was evident that the fish were well aware of the location of the best places to seek refuge.

An experiment was designed to determine the time required by juvenile manini to recognize and accept a new site of cover. A small opaque plastic bowl was inverted and placed with one edge elevated from the bottom of a 23 gal. aquarium in which 12 manini, 26 to 39 mm. in standard length, had been kept without a place of shelter for 3 days. Initially this bowl was avoided by all the fish. Fifteen min. elapsed before any fish swam near it. One hr. after the bowl had been added to the tank, the manini were frightened by rapid arm movements all around the aquarium; however none sought refuge in the new shelter. Upon being similarly frightened 3 hr. later, 2 of the smallest fish went into the bowl. Three hr. after this, all of the manini swam to the bowl for cover.

Adult manini are less inclined to seek shelter. Their reaction to an approaching swimmer usually takes the form of retreat. When cover is sought, the hole into which the fish swim usually has two or more entrances. As has been pointed out by Breder (1949*b*: 97) a reaction to attack which alternates between flight and hiding is common among fishes.

Fighting

Juvenile manini may often be seen fighting among themselves in the natural environment. Also, several days after being placed in an aquarium, this behavior becomes noticeable. It increases with time to the extent that it interferes with feeding. After 2 weeks in an aquarium, fully half the diurnal time of 12 juveniles was spent at this activity. The fighting was not associated with territoriality, but took place among all the fish and in all parts of the tank. Three of the larger fish were consistently the aggressors, and the smaller fish usually bore the brunt of their attack, but no definite peck order was established. When only 2 fish were present, however, the larger invariably dominated the smaller and forced it to remain in a corner of the aquarium for much of the day.

A distinct color change, which results in an almost complete reversal of the usual color pattern, accompanies the fighting. The broad pale interspaces between the vertical black bars become very dark, and the upper seven-eighths of the bars change to yellowish white except for a fine dark line in the center of each. On the lower eighth of the body the black bars are faintly visible in their normal width. The more aggressive fish are darker than the less aggressive ones.

The fighting usually involves little actual contact between fish. Most of the time a fish under

attack hastily withdraws, a response which generally satisfies the attacker for the moment. When there is no immediate retreat the two fish circle at close quarters and make pugnacious movements, mostly with the posterior part of the body. When a new manini was placed in the tank, it was attacked with ferocity by all of the other manini, but rarely more than one at a time. The hapless fish was pecked over the head and body, strongly bumped, and lashed at with the caudal spines of the others as it scurried from one part of the tank to the next. A manini twice the size of any in the tank was given the same treatment. After about half hour of incessant attack, this oppressed fish was observed to lie on its side on the bottom and submit completely to the relentless abuse. It was caught and examined shortly thereafter. Only a few small scratches on the fins and two small cuts on the body could be seen. The manini has a much smaller caudal spine than other species of *Acanthurus* and is not capable of inflicting much damage with it. Also the jaws do not seem strong enough to injure other fishes of equal size.

Manini were never observed to fight with other species of fishes. They appear to display a dominant behavior pattern to at least some, however. Six small pomacentrids (*Abudefduf abdominalis*) ranging from an estimated 18 to 38 mm. in standard length were observed to intermingle with 4 juvenile manini about 28 to 36 mm. in standard length at the shore of the Ala Wai Yacht Basin. Although the pomacentrids swam close to one another, they usually avoided coming within a body length of any manini. When one did and this was observed by a manini, the latter responded by a slow sideward movement of the body toward the intruding fish. The posterior half of the manini's body was curved toward the pomacentrid and vibrated slightly. The pomacentrid invariably retreated a short distance.

Breder (1948: 293) observed similar behavior in an aquarium with *A. chirurgus*. He noted that a peck order was established among certain fishes in an aquarium. This involved 4 pomacentrids and 1 gerrid. A small specimen of *A. chirurgus* was added which was about equal in size to the largest pomacentrid. Although the surgeonfish was not bothered much by the other fish at first, it seemed to be low or lowest on the peck order. It was never noted to pursue the others, but was occasionally pecked at by the others. Fourteen days later the peck order was modified and the acanthurid was definitely number one. There was little fighting but all kept clear of the surgeonfish which "showed" its peduncular spine to the more timorous.

I have never observed fighting among adult manini. Larger individuals may display dominance over smaller ones, however.

Behavior at Night

At night, both in the natural habitat and in the aquarium, manini rest on the bottom, usually with the pelvic fins and anal fin touching the substratum, in what appears to be a state of torpor or sleep. In general the body color is darker than during the day. Large dark blotches which may be seen faintly during the day between the vertical dark bars are more conspicuous at night. This resting phase is not without movement, for the pectoral fins are almost in constant slow motion and there are vertical undulations of the median fins. When a light was flashed on a darkened aquarium at night, short movements over the bottom were occasionally found to be in progress. These were directed backward more often than forward.

Usually the manini in an aquarium or a tide pool at night are well dispersed. In the normal environment most of the fish choose a sheltered although not a confining location. Many, however, may be seen in very exposed locations. Breder (1948: 294) observed that *A. chirurgus* rested on the bottom of an aquarium at night in the proximity of some shells, but in no case did it enter or hide in the shells.

If light is turned on a sleeping manini at night, and no sharp movements are made, the fish can be lightly touched or even picked up without its making any effort to escape. If a sharp movement is made in the water of the aquarium, or if the fish is roughly handled, it will dart away for a considerable distance over the bottom. This behavior was put to good use for the collection of this species alive. Using a head lamp at night to locate a sleeping fish, a dip net was cautiously placed in front of the

quarry. A long stick was used to prod the posterior end of the fish which often responded by swimming into the net.

The following observations on sleep were made on 10 juveniles, 27 to 40 mm. in standard length, which had been maintained in an aquarium for 12 days.

With the onset of darkness the fish settled to the bottom of the tank, although they continued to move about, and occasionally these movements would take them above the bottom. After total darkness ensued, 25 min. were required before they entered the state of suspended animation completely. This state was ascertained by lightly stroking the fish with a glass rod. When they ceased to flee from such contact, it was assumed that they were asleep. Since the period of attaining sleep was prolonged by the interruptions, a series of observations on successive nights was necessary to determine the normal period.

The stimulus to sleep was shown to be the onset of darkness and not merely the passage of a definite number of hours of diurnal existence, for the manini remained active for many hours when a light was kept burning above the tank after darkness set in. In one experiment the fish were kept awake for a period of 24 hr. They remained active during the time; however they ceased to feed toward the end of this period and displayed "restless" swimming.

When the fish were kept in total darkness for 24 hr., they remained relatively quiet on the bottom during the entire period. At the end of this period, however, it was noticed that they perceived the immersion of a hand into the tank regardless of how slowly it was inserted.

After 3 hr. of uninterrupted sleep, beginning with onset of darkness, lights were turned on to see how long the state of torpor would persist. In 13 to 14 min. the first 3 fish awakened and began to swim around the aquarium. These were the largest of the 10 manini. The remaining fish awakened according to size; the 2 smallest required 25 and 28 min., respectively. All of the fish displayed very restless swimming, moving constantly back and forth in the aquarium. When the lights were turned off, they required 39 min. to re-enter the state of torpor. No distinction could be detected in the time needed for the different-size fish to go back to sleep.

SUMMARY

1. In the Hawaiian Islands the common surgeonfish, *Acanthurus triostegus sandvicensis* (known in Polynesia as the manini), is found in many different habitats, although never far from coral or rock for shelter and algae for food. The young are abundant in tide pools.

Manini are not numerous in regions of heavy coral cover, although certain other surgeonfishes are surprisingly common there.

2. The eggs and larvae of the manini are pelagic. Eleven acanthurid larvae, 4.2 to 8.7 mm. in length, were taken in eight plankton tows 10–140 mi. from the nearest Hawaiian island. All were from the upper 50 m., although more tows were made in from 100 to 300 m. A higher percentage of acanthurid postlarvae have been found in surface-caught yellowfin tuna than those taken with long line at depths of about 30 to 160 m. Acanthurid larvae are more commonly found in the stomachs of tuna caught inshore than offshore.

3. The limits of temperature tolerated for 1 hr. by manini (both young and adults) appear to be about 12° and 37° C. Chlorinity tolerance for 24 hr. approximates 1.4 ‰ to 37 ‰. The most extreme readings of temperature found on Oahu in waters inhabited by manini were 16.2° and 35.1° C. and of chlorinity, 2.65 ‰ and 21.3 ‰.

4. Apart from the postlarval acanthurids found in tunas nothing is known of predation on the pelagic stages of the manini. In Hawaii, juvenile manini probably constitute prey to carangid, muraenid, synodid, scorpaenid, sphyraenid, cirrhitid, holocentrid, and antennariid fishes, and possibly certain large crabs. In view of the paucity of large piscivorous fishes in Hawaiian waters adult manini are probably relatively free of predation (man excluded).

5. The manini was found to be parasitized by one species of hydroid, four trematodes, four nematodes, two leeches, and six copepods.

6. Difficulty was experienced at one time maintaining manini in aquaria. They died in

about 48 hr., displaying large sores, eroded fins, and excessive mucus on the body. The dominant bacterium was a short, gram-negative rod.

7. The stomachs of 3 postlarval manini 6.7 to 7 mm. in length were examined for food. Two were empty, and 1 contained two appendicularians and a larval polychaete. Of 57 manini in the acronurus (late postlarval) stage taken by night light offshore, 45 were empty, and the rest contained only occasional fish scales or crustacean fragments lodged in intestinal folds, thus suggesting that the acronuri do not feed at night. The guts of 4 unidentified acronuri taken from a skipjack stomach caught during the day were filled with zooplankton.

8. During the first day of transformation from the acronurus to the juvenile state, most manini do not feed at all. Feeding on algae becomes progressively heavier as transformation continues.

Juvenile and adult manini feed almost entirely on relatively fine filamentous algae of numerous species. Little inorganic sediment was seen in the gut contents. When 28 different kinds of algae plus diatoms were offered to manini in feeding experiments, a red alga (*Polysiphonia* sp.) and a green (*Enteromorpha* sp.) were preferred. All of the blue-greens, the red *Asparagopsis*, and one species of the brown alga *Ectocarpus* were not ingested (although these may be found in stomach contents, mixed with other algae).

9. Juvenile manini were maintained in aquaria on algae alone. Fish 26 to 31 mm. in standard length grew at the rate of about 6 mm. per month (temperature 23.0° to 23.8° C.) when fed either *Polysiphonia* sp. or *Enteromorpha* sp.

10. Manini feed almost constantly during the day, and a large volume of algae is passed through the gut. Four juveniles weighing a total of 8.3 grams consumed 10.8 grams of *Enteromorpha* in 1 day and 8.8 the next. Two adults weighing 83.2 and 94.5 grams ate a total of 27.4 grams of *Enteromorpha* in 1 day. The adult fish did not feed as frequently in aquaria as in the natural environment. The larger fish dominated the smaller one and consumed the major part of the algae.

11. Manini showed no response to extracts of algae, and the visual sense alone is needed to locate algal food. The olfactory sense appears to function in feeding only to avoid unsavory material. Chemoreceptor organs in the mouth and possibly tactile organs as well seem to be associated with the acceptance of algae and the rejection of material not utilized as food.

12. The morphology of the digestive system is briefly discussed. The alimentary tract increases nearly three-fold during the 4 or 5 days of transformation from the acronurus to the juvenile form, reflecting a change in food habits from feeding on zooplankton to feeding on algae. The length of the gut increases from about three times the standard length in small juveniles to nearly six times in large adults.

13. Algae passed through the gut of juvenile manini in 1 hr. 45 min. and in about 2 hr. in adults. At night when feeding ceases, the gut is emptied slowly.

14. Although sustaining growth, the *Enteromorpha* appeared little affected after passing through the gut of manini. Additional work is needed to determine what is utilized by the manini from its algal food.

15. The stomach of the manini varies from slightly acidic to slightly alkaline. The intestine is alkaline (pH 7.7 to 9.1) and the gall bladder acidic (pH 6.2 to 6.4).

Amylase was detected throughout the digestive tract, strongest in the pancreas and weakest in the stomach. The pH optimum of the amylase is about 6.7. Maltase was not found.

Lipase, with a pH optimum of 7.2, was found in all digestive organs, strongest in the pancreas and pyloric caeca and weakest in the stomach.

Proteolytic enzymes are weak, especially from the stomach; pH optimum of pancreatic protease is about 8.4.

16. About two-thirds of the adult manini caught in unbaited traps off Oahu in from 30 to 90 ft. are males. Of 221 manini in museum collections from the tropical Pacific mostly taken from inshore waters, 134 (60.7 per cent) are females.

17. Although ripe males may be taken throughout the year (fewer, however, in the fall), ripe female manini have been found in Hawaii only from early December to late July (and transforming young from middle February to early October). Average monthly sea surface tempera-

tures in the Hawaiian Islands vary from about 75° to 81° F. Enlargement of the gonads appears to coincide with decreasing water temperature in the fall.

18. An estimate of about 2½ months for the duration of larval life of the manini in Hawaii was made by noting the time between the finding of the first ripe females and first transforming young of the season and the last ripe fish and last incoming acronuri.

19. Ripe female manini (*Acanthurus triostegus triostegus*) were found in collections made at islands of the tropical Pacific (where mean sea surface temperatures exceed 80° F. throughout the year) in all months of the year, as were transforming or early juvenile specimens, thus indicating year-round spawning in more equatorial waters.

20. A lunar periodicity in the number of transforming manini was discovered from tidepool collections on Oahu, with the peak in spring occurring a few days before new moon. Since a collection of young from the Gilbert Islands, where water temperatures average about 7° F. higher (and hence development is probably more rapid), indicates peak influx of acronuri approximately at the time of full moon, the periodicity is not attributed to any lunar effect on the young but to greater spawning by adults at one time of the month than another. Thirty-nine ripe female fish were found among 2,552 adult manini examined from 12 days before to 2 days after full moon during the spawning season and 4 among 1,311 fish seen in the remaining half of the lunar month.

21. Individual manini appear to spawn more than once during the season. Large and small ripe females were found near the start and end of the season. No completely spent ovaries were observed until July and August. In graphs of egg diameters of mature ovaries, a mode of egg size about intermediate to the diameter of transparent ripe eggs and primordial ova was invariably present during the season.

No specimens were found with modes of egg size lying between the intermediate-size mode and that of fertilizable eggs, thus suggesting that ripe eggs develop rapidly from the opaque ova of the intermediate group.

22. Although the spawning of manini was never witnessed in the Hawaiian Islands, *A. triostegus triostegus* was observed to spawn in the Tuamotu Archipelago. Several hundred fish were seen in a milling aggregation at dusk during the time of full moon. Many had broader bars on the body and darker fins than normal; 5 of these were speared and proved to be ripe males. Two normally colored manini were females, 1 running ripe. Spawning occurred at the apex of sudden rapid upward movements by small groups of fish. A current carried the eggs to the open sea.

23. The smallest running ripe female manini which was found on Oahu was 101 mm. in standard length; the smallest male, 97 mm. Manini probably do not spawn in their first year.

24. The number of ripe eggs in the ovary of one 123 mm. manini was estimated at 40,000.

25. Early development was studied following artificial fertilization of the eggs. The eggs average 0.67 mm. in diameter, have a single oil globule, and float at the surface. Hatching occurs in 26 hr. at 24° C. As yolk is used up, the larvae show a progressive tendency to sink. They combat this by upward swimming movements. Feeding begins at the age of 5½ days. No young were maintained in aquaria more than 6½ days; however, 3 postlarval manini, 6.6 to 7 mm. in total length, could be identified from plankton collections by fin-ray counts. The most striking feature of their morphology is very elongate second dorsal, second anal, and pelvic spines.

26. Manini acronuri come into shoal water to transform only at night. They are discoid, scaleless, and transparent with a silvery abdomen. Their second dorsal, second anal, and pelvic spines are poisonous. During transformation, which requires 4–5 days, adult-type configuration and coloration is attained, scales form, and the venomous quality of the spines disappears.

27. Light appears to be essential to transformation. Two acronuri taken at midnight were placed in a darkened 2½ gal. battery jar. They failed to transform, whereas 3 others in a comparable but not darkened container completed their metamorphosis to juvenile form.

28. A variation in standard length from 22 to 29.5 mm. was noted in 175 manini acronuri from Oahu in their first day of transformation. One hundred and sixteen were collected in tide

pools from 5 days before to 5 days after peak tide-pool recruitment (2 days before new moon). When the lengths of these manini were compared with the lengths of the 59 acronuri from the rest of the lunar month, a smaller range of length (23.5–28.5 mm.) was apparent for the former group in spite of nearly twice as many specimens. Presumably individual acronuri are capable of transforming some days before the rest of their age group, and hence at a smaller size, when they come inshore earlier than the others. Similarly, those which reach shoal waters later than the majority will have attained larger than average size.

29. A variation in size at transformation was found with locality which appears related to water temperature. The smallest size occurs in the warmest regions (about 20 mm. in the East Indies) and the largest in cooler sectors (Phoenix Islands excepted).

In the Hawaiian Islands the size at transformation averaged 26.3 mm. for 39 specimens collected in April and May and 25.4 mm. for 38 specimens which were taken from July to October (thus developing during warmer months).

30. Growth of juvenile manini, as determined by rearing of captive fish, recovery of fish marked by clipping rays from the top or bottom of the caudal fin, and progression of modes in successive graphs of tide-pool collections on Oahu is about 12 mm. per month.

The recovery of 281 manini of 1,247 tagged with Petersen disk tags fastened with monofilament nylon provided information on the growth of larger fish. The growth of adults 100 to 120 mm. in standard length is slightly greater than 1 mm. per month; 120 to 141 mm. fish grow about 0.8 mm. per month.

Growth of both juveniles and adults ceases during the winter months in the Hawaiian Islands.

31. No annular marks could be detected on the scales, otoliths or vertebrae of manini from which estimates of age could be made. Two larger acanthurids, *Naso unicornis* and *Acanthurus xanthopterus*, lived 20 and 15 years respectively in the Waikiki Aquarium in Honolulu where they died as the result of accidents.

32. Small juvenile manini tend to remain in the tide pool or shallow water area to which they first come as acronuri. With increasing size they move seaward.

Locality data from the recovery of tagged adult manini was too general to determine local movements, but adequate to demonstrate that no extensive migrations are normally undertaken by this surgeonfish. If displaced from their home area, however, manini are capable of wandering distances as great as 8 mi.

33. Manini may be seen as solitary fish, in small groups, or in large feeding aggregations. One large group of fish, although observed to remain in one region in the Tuamotus, moved as much as 300 yd. in several hours.

34. Juvenile manini in a large tide pool on Oahu were observed to have two hiding places beneath ledges, one of which was preferred. In order to attain shelter they will swim toward an intruder, if necessary. From 4 to 7 hr. were required for aquarium fish to accept an inverted bowl tilted on edge as shelter.

Adults are less inclined to seek shelter. Their reaction to an approaching swimmer usually takes the form of retreat.

35. Juvenile manini frequently fight among themselves, both in the natural environment and after being adapted to aquarium life. This does not concern territoriality, but is an expression of dominance by larger fish over smaller fish or old residents (in the case of aquarium fish) over new arrivals. A distinct color change, which involves an almost complete reversal of color pattern, is readily apparent, with the more aggressive fish becoming the darkest. Generally there is no contact between fish, and the fish under attack usually retreat. If not, there is a circling at close quarters with occasional overt movements, especially with the posterior part of the body. The manini's caudal spine is small, and the juveniles were observed to inflict at most only superficial scratches.

Manini were not observed to fight with other species but they may display a dominance in their behavior towards some.

36. With the onset of darkness juvenile and adult manini settle to the bottom, usually with pelvic and anal fins in contact, and enter a state of torpor or sleep. Occasional short movements are made, these more often directed backward than forward. Even when remaining in one place

the pectoral fins are kept in slow motion and there are vertical undulations of the median fins. The color is darker than during the day, and large dark blotches are conspicuous between the vertical black bars on the body. A period of 25 min. after darkness ensued was found to be necessary for the fish to reach a state when they could be lightly touched without fleeing. When lights were kept on in an aquarium for 24 hr., manini remained active, however they ceased to feed toward the end of this period and swam restlessly. A light was turned on after 10 manini, 27 to 40 mm. in standard length, were allowed to sleep for 3 hr. From 13 to 28 min. were required for the fish to awaken, the smallest taking the longest time.

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A New Species of *Micronereis* (Annelida, Polychaeta) from the Marshall Islands[1]

DONALD J. REISH[2]

DURING THE COURSE of surveying Eniwetok Atoll, Marshall Islands, for polychaetous annelids in the summers of 1957 and 1958, the author encountered from three localities four specimens of a new species of polychaete belonging to the nereid genus *Micronereis* Claparède. Transects were made of both the ocean and lagoon sides of the islands shown in the map of Eniwetok Atoll (Fig. 1). One of the collecting methods employed was to preserve algae, coral, rocks, sand, etc., in formalin in the field and to sort out the polychaetes in the laboratory. The new species of *Micronereis* was collected in this manner.

FAMILY NEREIDAE

Micronereis Claparède

Micronereis eniwetokensis n. sp.
Figs. 2–6

Four complete specimens, each with 17 setigerous segments measuring 1.5 to 2.0 mm. in length, came from three localities in Eniwetok Atoll. The prostomium (Fig. 2) is broadest posteriorly and is clearly separated from the first setigerous segment. The prostomium is weakly indented at its anterior margin. Four pairs of tentacular cirri are broadest near the point of attachment and tapered distally. The short palpi are viewed from the ventral side. There are no prostomial tentacles or peristomium as is characteristic for the genus.

Four large eyes are in trapezoidal arrangement, with the anterior pair being the larger, farther apart, and provided with a clear lens. A variation was noted in the eyes of one specimen (Fig. 3). The anterior pair was elongated and extended posteriorly and laterally to the second pair. Each anterior eye was provided with a large clear lens.

The yellow jaws (Fig. 4) were seen by dissection or by mounting the worm in glycerine. They were broadest at their base and terminated in one large tooth and three smaller teeth. The apical tooth was serrated along its inner margin.

The first two setigerous segments are uniramous with homogomph spinigers. Each has a filiform ventral cirrus.

All parapodia (Fig. 5) are biramous from the third setigerous segment to the posterior end. The rami are widely separated and each has a single black aciculum. The inner margin between the notopodium and neuropodium is ciliated. Each ramus has a cirrus; the dorsal one is longer than the ventral one.

All setae (Fig. 6) are homogomph spinigers with the appendages lacking spines along their margins. The setae number 12–20 in each lobe of the parapodium.

The pygidium is characterized by having a bilobed ventral fleshy membrane and two blunt lateral lobes.

DISCUSSION

Three species are previously known for the genus *Micronereis*, *M. variegata* Claparède 1863, *M. nanaimoensis* Berkeley and Berkeley 1953, and *M. halei* Hartman 1954. Sexual dimorphism has been described for the former two species. Specialized setae in the third setigerous segment of the male, and a difference in the number of segments between the two sexes, occur in both *M. variegata* and *M. nanaimoensis*. The jaws vary according to sex in *M. variegata*. Additional dimorphic characters in *M. nanaimoensis* include the pygidium, coloration, and capillary setae in

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the male. Sexual dimorphism is unknown for *M. halei* and *M. eniwetokensis*.

The large anterior eyes (Fig. 3) on one individual of *M. eniwetokensis* are an unusual variation for the members of the genus. The appearance of secondary sex characteristics, such as enlargement of the eyes prior to sexual maturity, is widespread in the family Nereidae (Reish, 1957), but it is unknown for the genus *Micronereis* (Berkeley and Berkeley, 1953; Rullier, 1954). No other morphological differences were noted in this specimen collected from 94 ft. of water in the lagoon.

M. eniwetokensis comes closest to *M. varie-*

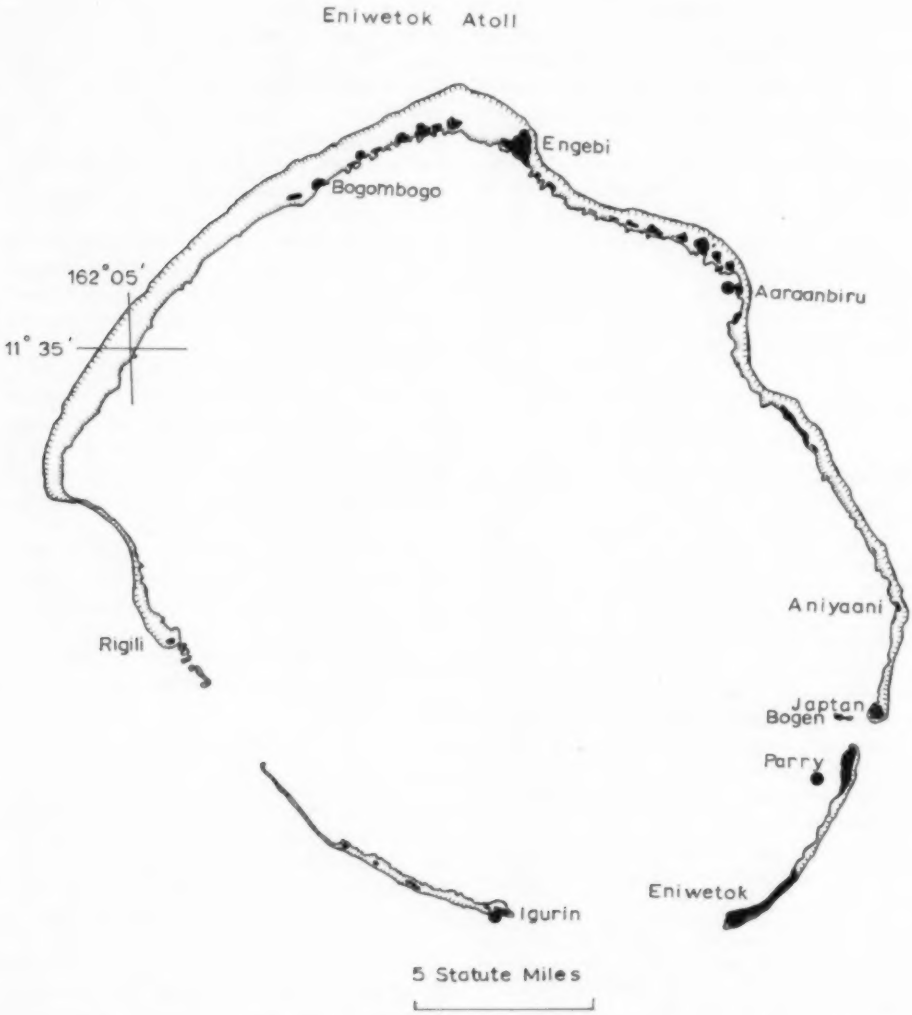
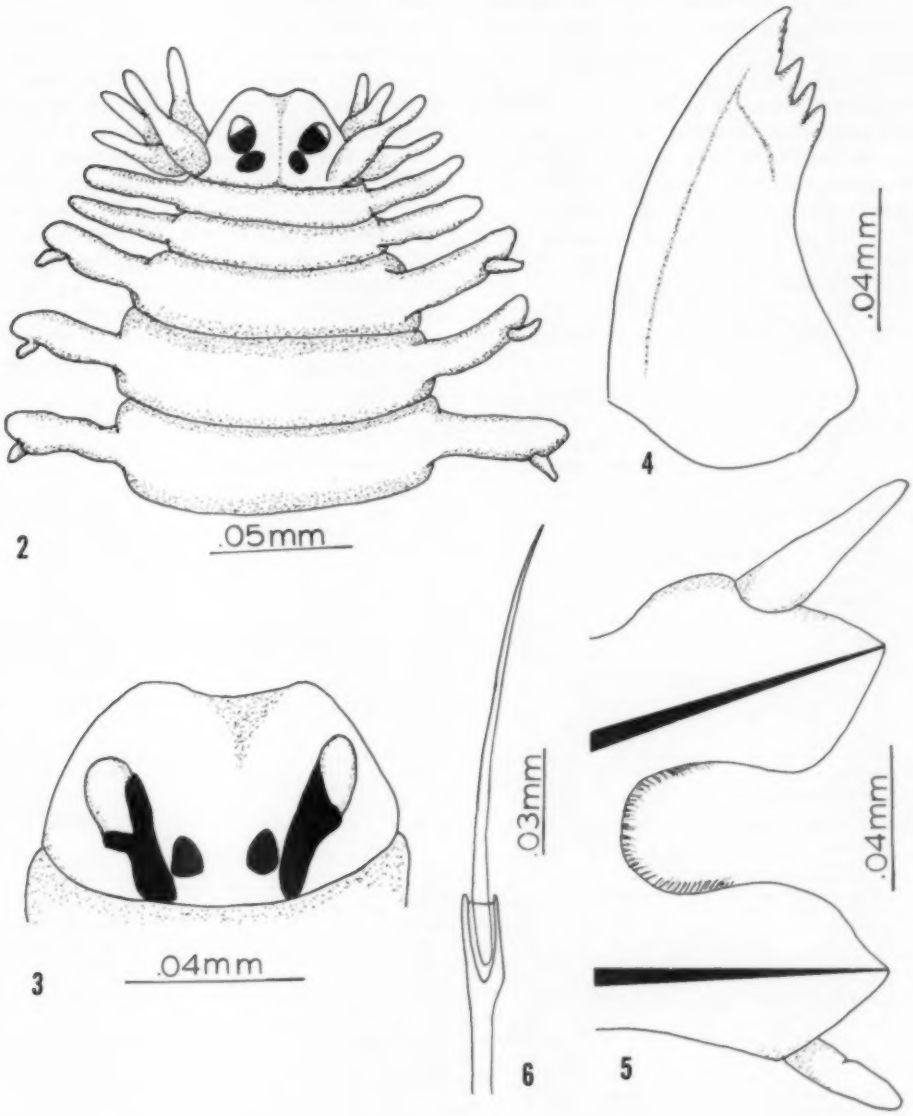


FIG. 1. Map of Eniwetok Atoll, Marshall Islands. Collections were made at the named islands. *Micronereis eniwetokensis* was collected from the areas indicated by the dots.



FIGS. 2–6: 2, Anterior end of the holotype of *Micronereis eniwetokensis;* 3, prostomium of *M. eniwetokensis* with enlarged eyes; specimen collected from a depth of 94 ft. in the lagoon of Eniwetok Atoll; 4, jaw of *M. eniwetokensis;* 5, parapodium from the mid-region of *M. eniwetokensis;* setae omitted from figure; 6, homogomph spiniger from the notopodium of Figure 5.

gata; they differ in the nature of the homogomph spiniger, the pygidium, and the presence or absence of cilia on the parapodia. There are some distinct characteristics for the male of *M. variegata*; it is not known whether or not sexual dimorphism occurs in *M. eniwetokensis*. The diagnostic characters for the known species of the genus are summarized in Table 1.

TYPE MATERIAL: The holotype, one paratype, and two additional specimens have been deposited in the U. S. National Museum.

TYPE LOCALITY: Intertidal region on the lagoon side of Aaraanbiru Island, Eniwetok Atoll, Marshall Islands (Fig. 1).

ECOLOGY: As stated above, pieces of coral rock of loose substrate were preserved in the field at each station visited. *M. eniwetokensis* was collected in this manner. It was associated with the following species of polychaetes:

Aaraanbiru Island, lagoon side, substrate coral rock and beach rock with algae attached. Polychaetes: *M. eniwetokensis* (2 specimens), *Haplosyllis spongicola* Grube (1), *Opistosyllis longicirrata* Monro (6), *Ceratonereis mirabilis* Kinberg (17), *Eunice afra* Peters (1), *Lysidice collaris* Grube (3), *Palola siciliensis* Grube (3), *Dodecaceria laddi* Hartman (2), and *Polyophthalmus pictus* (Dujardin) (19).

Igurin Island, ocean side, substrate coral rock and fragments taken from under coral head near surge zone. Polychaetes: *Micronereis eniwetokensis* (1 specimen), *Eurythoë complanata*

TABLE 1

COMPARISONS OF THE KNOWN SPECIES OF *Micronereis*

CHARACTERISTIC	*M. variegata*	*M. nanaimoensis*	*M. halei*	*M. eniwetokensis*
Length	2–4 mm.	13–15 mm.	7 mm.	1.5–2.0 mm.
Number of setigerous segments ♂ ♀	 17–18 21	 23 26	 20–25 (sex unknown)	 17 (sex unknown)
Palpi	absent	present	present	present
Jaws	dimorphic; ♂ 5 teeth ♀ 4 teeth	4–5 teeth	6 teeth	4 teeth
Crotchets in ♂, third segment	2 curved	5+ crested	unknown	unknown
Spines on appendage of homogomph spinigers	present	present	absent	absent
Cilia on parapodia	absent	present	absent	present
Pygidium	2 anal cirri	2 anal cirri in ♂ and ♀; also 2 lateral lobes in ♂	——	2 lateral lobes; ventral bilobed membrane
Unique pigmentation	none	2 red bands on tentacular cirri; see original account for body pigmentation	brown band on tentacular cirri	none
Unique characters	none	capillary setae in ♂	inferior notopodial and superior neuropodial lobes in parapodium	none
Geographical distribution	Europe, Mediterranean Sea	British Columbia, Canada	South Australia	Eniwetok Atoll, Marshall Islands

(Pallas) (2), *Pseudeurythoë oculifera* (Augener) (1), *Genetyllis gracilis* (Kinberg) (1), *Typosyllis variegata* (Grube) (2), *Platynereis pulchella* Gravier (6), *Lysidice collaris* (1), *Palola siciliensis* (1), *Dodecaceria laddi* (2), and *Terebella ebrenbergi* Grube (1).

Parry Island, lagoon side in 94 ft. of water collected by Mr. Mike Chamberlain, 450 ml. of light gray sand. Polychaetes: *Micronereis eniwetokensis* (1 specimen), *Micronephthys sphaerocirrata* (Wesenberg-Lund) (2), previously known only from the Sea of Iran (Wesenberg-Lund, 1949), and *Scolelepis indica* Fauvel (2).

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Life Cycle of *Mesostephanus appendiculatus* (Ciurea, 1916) Lutz, 1935 (Trematoda: Cyathocotylidae)[1]

W. E. MARTIN[2]

FOR A NUMBER OF YEARS, the author has been studying trematode larvae which develop in the California horn-shell snail, *Cerithidea californica* Haldeman. One of these, a pharyngeate, furcocercous cercaria, proved to be the larva of *Mesostephanus appendiculatus*. The adults of this species were first described from the small intestines of Rumanian cats and dogs by Ciurea (1916). Ciurea, however, placed this species in the genus *Prohemistomum*. Price (1928) found this parasite in the small intestine of a dog that had lived in the vicinity of Washington, D.C. Lutz (1935) transferred this and some other species to his new genus, *Mesostephanus*, naming *M. fajardensis* (Price, 1934) as type species. Dubois (1953) includes the following species in the genus *Mesostephanus*: *M. fajardensis* (Price, 1934); *M. appendiculatus* (Ciurra, 1916); *M. appendiculatoides* (Price, 1934); *M. cubäensis* Allegret, 1941; *M. haliasturis* Tubangui and Masiluñgan, 1941; and *M. longisaccus* Chandler, 1950. Caballero, Grocott, and Zerecero (1954) added *M. microbursa* from the intestine of *Pelecanus occidentalis californicus*. Dubois (1953) believes that the members of the genus are natural parasites of certain fish-eating birds and accidental parasites of dogs.

MATERIAL AND METHODS

Infected *Cerithidea californica* were isolated in finger bowls. Emerged cercariae were studied alive and as fixed and stained whole mounts. Cercariae were fixed without pressure by forcibly ejecting them into cold Bouin's solution. Earlier larval stages and percentages of infection were obtained by crushing snails. Uninfected *Fundulus parvipinnis parvipinnis* (Girard) and *Gillichthys mirabilis* Cooper were collected in an isolated pool where there were no snails. These fish were exposed to cercariae and, following a lapse of 2–3 weeks, were fed to hatchery-raised chicks. The chicks were examined 9 days after the experimental feeding. The adult worms obtained were fixed in Bouin's solution under slight cover-glass pressure. Larval and adult stages were stained with paracarmine and mounted in Permount.

All measurements are in millimeters.

OBSERVATIONS

The sporocysts and cercariae of *Mesostephanus appendiculatus* develop in the digestive gland of the brackish-water snail, *Cerithidea californica*. During a 12-month survey (Martin, 1955), in which at least 1,000 snails were examined each month, only 7 infections of this parasite were found in 12,995 snails.

SPOROCYST (Fig. 2): Mother sporocysts were not observed. Daughter sporocysts are saccular and elongate. Measurements of 20 stained and mounted specimens are: length 1.368–3.355, av. 2.38; maximum width 0.173–.302, av. 0.236. The wall of the sporocyst has transverse contractile bands. At intervals there are thicker bands which give a false appearance of segmentation. One end of the sporocyst has a thick wall which is traversed by a birth canal.

CERCARIA (Figs. 3, 4): The cercariae are nonoculate and furcocercous. Though they lack eyespots, they show positive phototropism. The body surface is covered with minute, quincuncially arranged spines and scattered papillae

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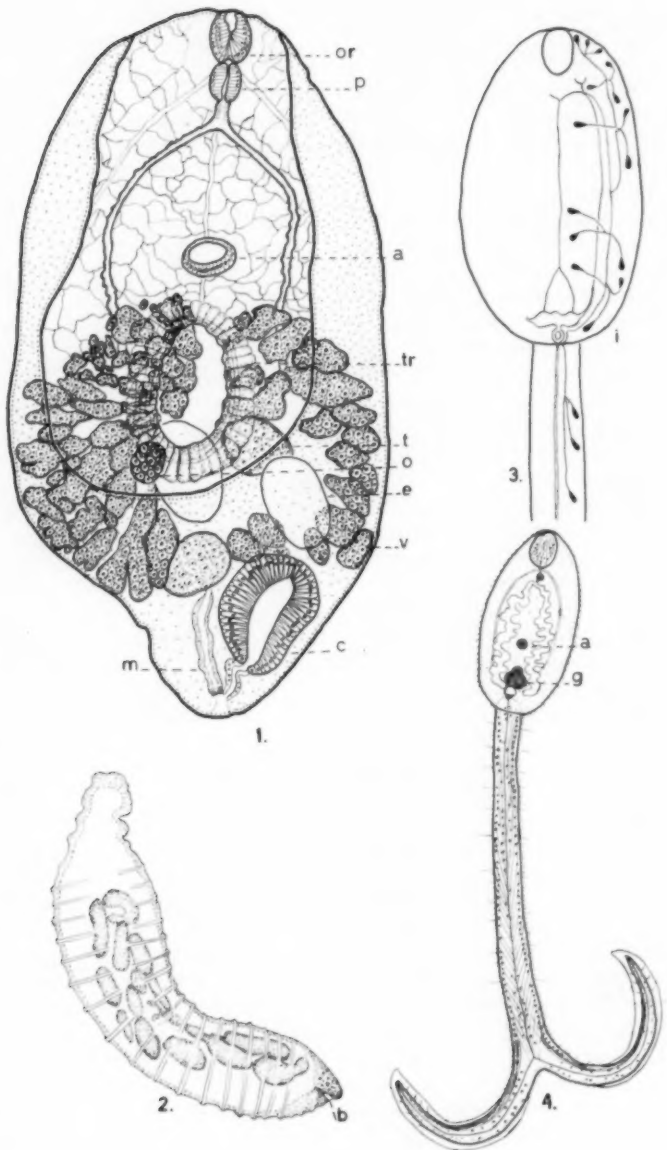
with bristles. Tubular glands are plentiful laterally and sparse dorsoventrally in the anterior half of the body. Ten to 12 glands have their cell bodies near the oral sucker and have ducts opening near the mouth. Measurements based on 20 stained and mounted specimens are: body length 0.18–.258, av. 0.192; maximum body width 0.078–.115, av. 0.094; oral sucker length 0.031–.045, av. 0.038; oral sucker width 0.025–.037, av. 0.03; ventral sucker midventral, rudimentary, 0.009–.012, av. 0.01 in diameter; lengths of prepharynx and esophagus approximate that of pharynx; pharynx oval to spherical, 0.006–.012, av. 0.011 long and 0.012–.016, av. 0.013 wide; intestinal caeca sinuous, terminating near excretory bladder; genital primordium median, immediately anterior to excretory bladder, 0.006–.022, av. 0.019 long and 0.019–.025, av. 0.021 wide; excretory bladder small, transversely elongate, with exit duct entering tail, dividing into two ducts which pass around the "Island of Cort" and rejoin, extending to the furcal region to divide into two ducts, each of which opens to the outside at the tip of a furca. Four collecting ducts empty into the bladder, two laterally and two medial to the lateral ducts on the anterior wall of the bladder. The two medial ducts pass around the genital primordium to unite and proceed as a single duct to a point near the bifurcation of the gut where it joins the lateral ducts which have proceeded anteriorly from the bladder. As the lateral ducts bend medially, each gives off a duct whose proximal portion contains a tuft of cilia. The latter duct extends posteriorly to about mid-body level where it divides into anterior and posterior branches each of which collects from three groups of three flame cells each. Three of the flame cells emptying into the posterior branch are located in the tail. The excretory formula is $2\ [(3+3+3)\ +\ (3+3+(3)] = 36$. Short, moniliform concretions occur in the main collecting tubes. The tail is set in a dorsal socket near the posterior end of the body. The tail surface bears bristles and minute spines. The tail stem length is 0.358–.407, av. 0.376, and maximum width near the junction with furcae 0.014–.022, av. 0.021. The furcae are 0.18–.2, av. 0.19 long and 0.019–.022, av. 0.021 in maximum width near the junction with the tail stem. Each furca bears a dorsoventral fin over the distal four-fifths of its length.

METACERCARIA: *Fundulus parvipinnis parvipinnis* and *Gillichthys mirabilis* were exposed to cercariae which rapidly penetrated the skeletal muscles and encysted. Penetration of large numbers of cercariae killed the fish. Death of the second intermediate host due to the penetration of large numbers of cercariae has been noted by Vernberg (1952) for a related parasite. Metacercariae approximately 3 weeks old were dissected from the fish and were fed, along with some muscle tissue, to hatchery-raised chicks.

ADULT (Fig. 1): Adult *Mesostephanus appendiculatus* were obtained from the small intestines of hatchery-raised chicks fed fish muscle and metacercariae. The chicks were examined 9 days after the experimental feeding. The following description and measurements are based on nine specimens. Body surface covered with scale-like spines arranged quincuncially. Body length 0.547–.763, av. 0.68; body width 0.346–.518, av. 0.41; oral sucker length 0.04–.059, av. 0.049; oral sucker width 0.047–.078, av. 0.055; acetabulum 0.04–.068, av. 0.06 in diameter; tribocytic organ well developed, opening usually slitlike; prepharynx very short; pharynx 0.037–.058, av. 0.05 long and 0.031–.044, av. 0.037 wide; esophagus approximately one-half pharyngeal length, with transverse muscle fibers; intestinal caeca sinuous, with occasional short diverticula, reaching to near posterior end of body; testes oblique, in posterior half of body, 0.109–.124, av. 0.116 long and 0.072–.087, av. 0.079 wide; cirrus sac and cirrus well developed; male genital opening communicates with common genital exit at posterior end of body; ovary intertesticular, 0.05–.08, av. 0.065 long and 0.04–.065, av. 0.05 wide; metraterm elongate, muscular, with sphincter at distal end where it empties into common genital exit; eggs yellow, operculate, 0.084–.137, av. 0.108 long and 0.058–.081, av. 0.07 wide; vitellaria composed of discrete follicles arranged in a circle in posterior half of body but not entering posterior conical body extension; excretory system more complex than in cercaria, anastomosing branches arise from main collecting ducts, some branches end blindly near body surface.



FIGS. 1–4: 1, Adult *Mesostephanus appendiculatus*, ventral view; 2, sporocyst; 3, diagram to show most of excretory system; 4, cercaria, ventral view. Abbreviations: *a*, Acetabulum; *b*, birth pore; *c*, cirrus sac; *e*, egg; *g*, genital primordium; *i*, Island of Cort; *m*, metraterm; *o*, ovary, or oral sucker; *p*, pharynx; *t*, testis; *tr*, tribocytic organ; *v*, vitellaria. All drawings made with the aid of a camera lucida unless otherwise stated.

DISCUSSION

The body dimensions of the adult *M. appendiculatus* described in this paper are smaller than those listed for the species by Dubois (1938). This may be due to the fact that the duration of the infection was only 9 days so that the worms probably had not attained their full size even though they were sexually mature. The range of egg size and the number of eggs (1–7) in the uterus were greater in my specimens that in those listed by Dubois (1938), which include measurements given by Ciurea (1916) and Prendel (1930). The anterior extent of the cirrus was greater in some specimens than is shown in Figure 1. The extent of the cirrus in Figure 1 resembles that of *M. microbursa* Caballero, Grocott, and Zerecero (1954), recovered from the intestines of pelicans, *Pelecanus occidentalis californicus*, collected in Panama and in the Coronado Islands off Mexico. However, the sucker ratio, spination, and extent of the posterior appendix are different in the two species.

The present work extends the range of *M. appendiculatus* to the west coast of the United States. It has been found on the east coast of this country by Price (1928), in Rumania by Ciurea (1916), and in the Ukraine by Prendel (1930).

Dubois (1953) states that pelicans are the natural hosts of this species. Since this parasite can develop also in dogs, cats, and chicks, the present author believes that other fish-eating birds probably serve as additional natural hosts.

Maxon and Pequegnat (1949) examined *Cerithidea californica* collected at Newport Bay, California, between October, 1947, and May, 1949. They found 21 per cent of the snails infected with furcocercous cercariae. They described one of the latter with 16 flame cells but did not describe the cercaria of *Mesostephanus appendiculatus*.

SUMMARY

The life cycle of *Mesostephanus appendiculatus* (Ciurea, 1916) Lutz, 1935 has been demonstrated experimentally. Sporocysts and cercariae develop in the brackish-water snail, *Cerithidea californica* Haldeman, collected at Newport Bay, California. The cercaria is furcocercous and has a flame-cell pattern expressed by the formula 2 [(3+3+3) + (3+3+(3)] = 36. Second intermediate hosts are *Fundulus parvipinnis parvipinnis* (Girard) and *Gillichthys mirabilis* Cooper. Experimentally infected fish were fed to hatchery-raised chicks. After a lapse of 9 days, egg-bearing worms were removed from the small intestines of the chicks.

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Some Notes on the Hawaiian Monk Seal

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UP TO 1958 the collections of the British Museum (Natural History) possessed neither skeletal material nor skin of the Hawaiian or Laysan monk seal, *Monachus schauinslandi* Matschie 1905. Indeed the only remains of this animal in Europe until now have been those brought back by Dr. Schauinsland, amongst which was the skull of the seal later named after him by Matschie (Matschie, 1905). The stuffed skin of this animal is in the Bremen Museum and the type skull is in the Zoological Museum in Berlin, no. 32795 (Wahlert, 1956). So it was with great pleasure that we received, in the summer of 1958, through the kindness of Mr. Vernon E. Brock, then director of the Territorial Division of Fish and Game, Honolulu, Hawaii, a young male monk seal from Laysan Island that had been shipped complete and frozen to this country. The animal was thawed, injected with coloured gelatin in the vascular system, and dissected after fixation, but unfortunately the tissues were too poorly preserved for any accurate histology.

DESCRIPTION

The seal is young, has a nose-to-tail length of 163.5 cm. (5 ft. 6 in.) and weighs 74.4 kg. (164 lb.) complete. Kenyon and Rice (1959) give the estimated weights of recently weaned pups as from 95–160 lb. The present animal was caught June 4, 1958, and as it must have been very near to being weaned, its probable date of birth must have been about April 30. Although the weight is a little high for a recently weaned pup, the animal is in very good condition and is unlikely to have been a yearling, as yearlings are relatively thin and do not reach the weight and condition of pups that have been feeding from their mothers. Similarly the state of the epiphyses and the obvious youth of the skeleton make it unlikely that it is from a 2-year-old animal. The age of the present animal is therefore estimated to be about 5 weeks (the thymus is large and weighs 32.5 g.). The coat is dark silvery grey dorsally, on the top of the head, on both sides of the fore and hind flippers, and on the dorsal surface of the tail. Laterally the grey shades to silvery white ventrally. The hind flippers are a little lighter grey on the inner side towards their insertion. There are also lighter patches round the eyes and surrounding the insertion of the supraorbital vibrissae, and along the upper lip. The lower jaw is light in colour. On the back the hairs are dark grey with a white tip. This white tip becomes longer towards the belly so that the ventral hairs are white with a short dark base. The moustachial whiskers are in five rows on each side of the nose, the upper row having four whiskers and the other rows approximately nine in each. The whiskers are dark brown at the base, shading to straw colour at the tip; they are oval in cross section and are not beaded as in *Phoca* (Fig. 1).

The tongue has a notch in its anterior end. The length of the small intestine is approximately 57 ft. The only food remains in the stomach are fish bones and skin and these have been identified as being most probably from the puffer fish, *Arothron meleagris* (Lac.), which is a poor swimmer usually found near coral formations. Nematodes, a small cephalopod beak, and an isopod are also present in the stomach. The nematodes have been identified as *Contracaecum turgidum*, a species previously described from this seal, and the isopod as *Livoneca* sp., usually found as an ectoparasite on fish and probably ingested attached to a fish. In the small intestine there are remains of a tapeworm. It is not in a sufficiently good condition to be identified exactly, but is probably *Diphyllobothrium* sp.

The skin and skeleton of this seal are in the collections of the British Museum (Natural History), the registered number of the skin being 58.521, and that of the skeleton 1958.11.26.1.

OSTEOLOGY

The skeleton of *M. schauinslandi* has not previously been described and although it is attempted here to fill this gap the description and

[1] British Museum (Natural History).

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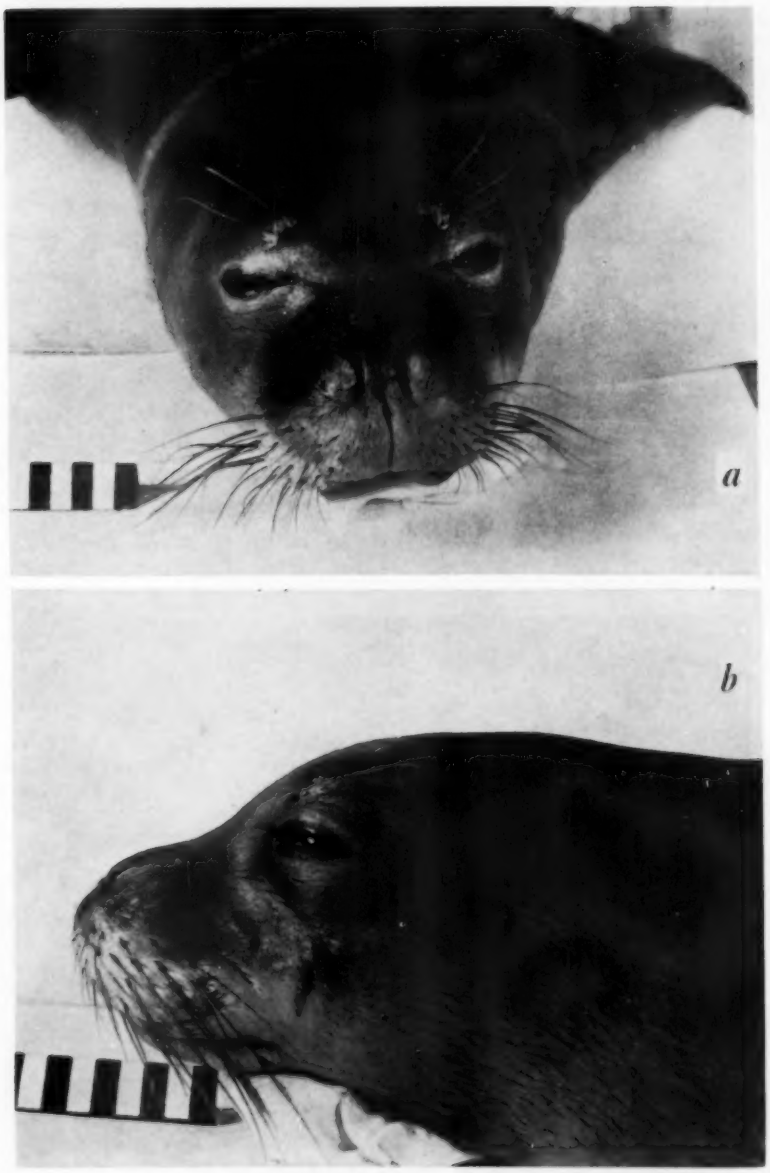

FIG. 1. *a*, Anterior view of the face of *M. schauinslandi*. *b*, Lateral view of the face, showing dorsal position of nostrils.

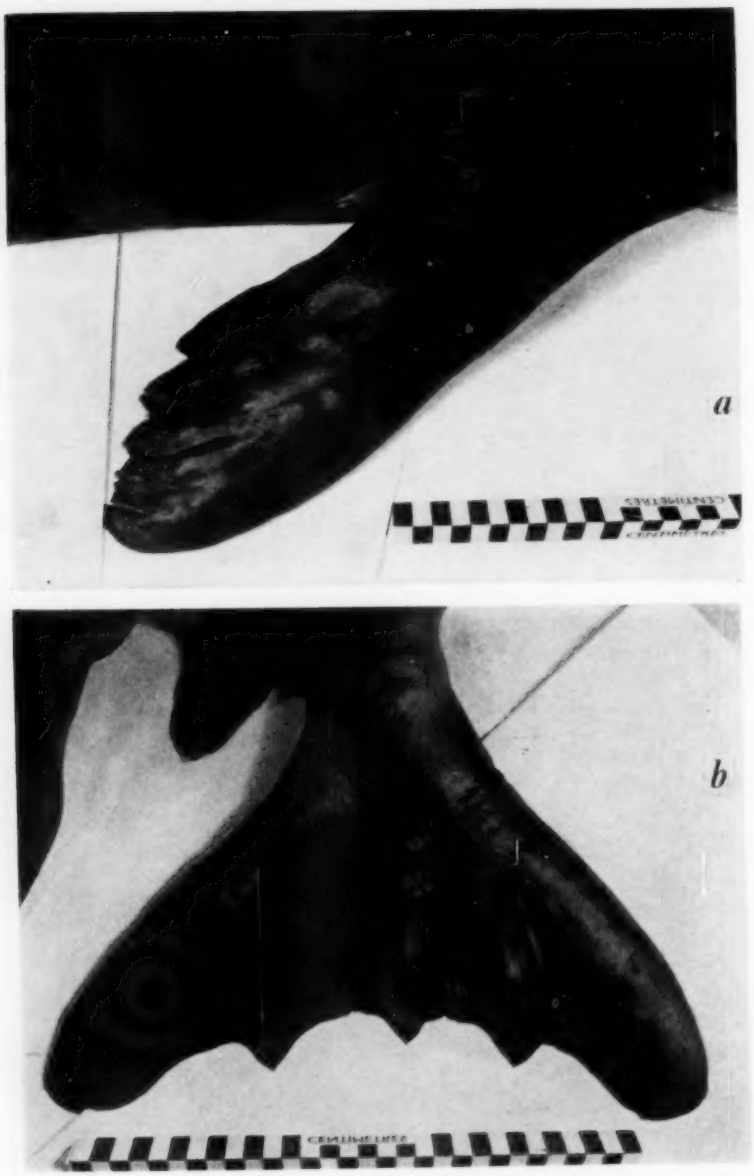

FIG. 2. *a*, Dorsal view of right fore flipper. *b*, Dorsal view of right hind flipper.

comparison are considerably limited by the youth of the specimen. The form of this description is based on that of the skeletons of *M. monachus* and *M. tropicalis* (King, 1956) and frequent reference will be made to the details in that paper. No skeleton of a young *M. tropicalis* was available so the *M. schauinslandi* skeleton was compared with that of an adult *M. tropicalis* (1887.8.5.1.) and of a young *M. monachus* (1894.7.27.3), the skull of which showed by its condylobasal length (224 mm.) and suture age (13) that it was from an animal of approximately the same size as the Laysan monk seal.

Comparison of M. schauinslandi *Skull with Those of* M. monachus *and* M. tropicalis

1. The additional measurements now available of the skull of *M. schauinslandi* confirm the previous statement (King, 1956) that skulls of both *M. schauinslandi* and *M. tropicalis* are slightly narrower in proportion to their width than those of *M. monachus*, though the accuracy of this conclusion is limited by the small number of skulls available.

	M. monachus	*M. tropicalis*	*M. schauinslandi*
	%	%	%
Zygomatic width	59.9–70.3	61.7–62.1	60.9–61.5
Snout width at canines	20.9–26.0	20.6–20.9	20.3–20.5
Width at external auditory meatus	53.1–58.5	49.8–50.5	50.5–55.0
Width at petrous bones	60.3–64.9	56.3–59.2	59.2–64.1

2. The nasal bones of this young animal are as previously described from the type skull. The anterior ends are in the form of an inverted V with the point directed posteriorly; the posterior ends do not taper as much as in *M. tropicalis*.

3. The lower edge of the infraorbital foramen is, when seen from the front, narrower than the upper edge. This confirms Matschie (1905) and is similar to *M. tropicalis*.

4. The absence of a maxillary tubercle at the anterior edge of the orbit also confirms Matschie.

5. As previously noted, the shape of the zygomatic arch is more like that of *M. monachus* than *M. tropicalis*.

6. It was noted previously that the posterior edge of the palate of *M. schauinslandi* formed a wide V. It is now felt that it is better described as U in shape and rather more like that of *M. monachus*, though there is probably a certain amount of variation in this character.

7. The pterygoid bones curve outwards as in *M. tropicalis* and in this young skull of *M. schauinslandi* they are just visible when it is viewed dorsally.

8. The coronoid process of the lower jaw is narrow and like that of *M. tropicalis*.

9. Examination and comparison of the young skull of *M. schauinslandi* now available confirms the previous report that it is more like *M. tropicalis* than *M. monachus* (Fig. 3). There are no supernumerary bones in the skull.

Kenyon and Rice (1959) note that, in the few skulls of *M. schauinslandi* they examined, the shape of the palate and the shape of the zygomatic branch of the squamosal do not appear to be constant and are thus not good distinguishing characters. It is certainly agreed that the shape of the palate is variable and there is a need for the examination of as many adult skulls as possible to determine the amount of variation.

Measurements of Skull of M. schauinslandi *1958.11.26.1*

	mm.	%
Condylobasal length	220	100
Condylobasilar length	211	95.9
Basal length	201	91.4
Basilar length	192	87.3
Snout width at canines	45	20.5
Width of skull at front end of last upper molars	59	26.8
Zygomatic width	134	60.9
Width at upper edge auditory meatus	121	55.0
Width at petrous bones (mastoid width)	141	64.1
Palatal length	101	45.9
Palatilar length	92	41.8
Width of occipital condyles	62	28.2
Length of nasal suture	50	22.7
Length of upper molar row	55	25.0

Suture age 13

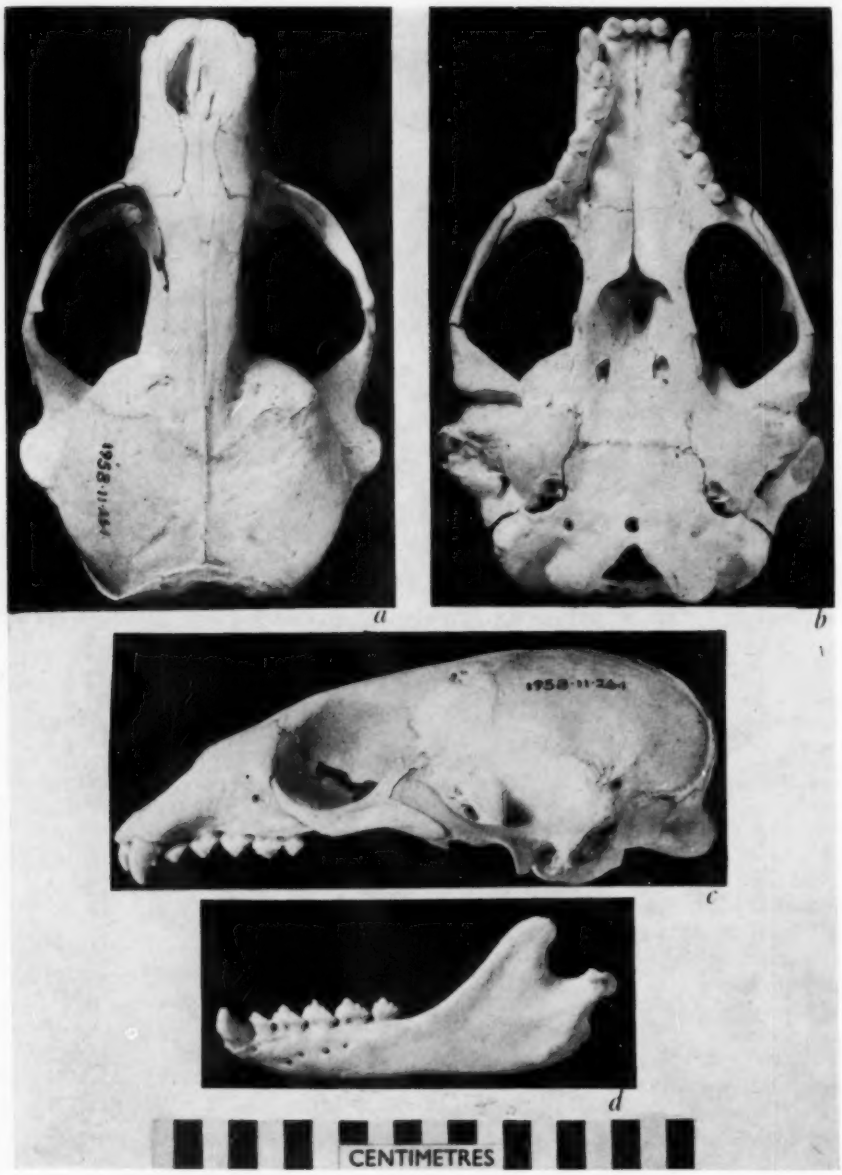

FIG. 3. *a*, Dorsal, *b*, ventral, and, *c*, lateral views of the skull of *M. schauinslandi*. *d*, Lateral view of lower jaw.

Teeth

Dental formula $\frac{i\ 2}{2}, \frac{c\ 1}{1}, \frac{pc\ 5}{5}$.

The term "post canines" is used here instead of "molars" and "premolars," as these latter cannot be used precisely when referring to pinniped teeth.

UPPER JAW TEETH: As previously mentioned, the upper incisors are set in a straight line across the anterior end of the premaxillae and in general the setting and shape of the teeth are like *M. tropicalis*. The incisors of this young animal do not have such a pronounced "waist" as those of the adult *M. tropicalis*, but it is more evident than in the young *M. monachus*.

The canines are very small for a male animal. Those of the young *M. monachus*, also a male, whose skull is only 4 mm. longer than that of the young *M. schauinslandi*, are much larger.

	M. monachus	*M. schauinslandi*
Anteroposterior length at crown-root junction	15 mm.	12 mm.
Anterior height of canine (in straight line from crown-root junction to tip)	23 mm.	14 mm.

M. tropicalis also has small canines. The measurements given below of the upper canines of an adult male *M. tropicalis* (1889.11.5.1; condylobasal length 267 mm., suture age 25) are compared with those of an adult male *M. monachus* of approximately similar size (1863.4.1.1; condylobasal length 273 mm., suture age 26).

	M. monachus	*M. tropicalis*
Anteroposterior length	16.5 mm.	11 mm.
Anterior height	27 mm.	est. 17 mm. (v. worn)

The height of the crown of the postcanine teeth in both *M. tropicalis* and *M. schauinslandi* is lower than in *M. monachus* and the main cusp is more rounded. In this respect *M. schauinslandi* is more like *M. tropicalis*, but in the possession of a single anterior and posterior cusp it resembles *M. monachus*. The fourth postcanine has, however, two small anterior cusps and two small posterior cusps. The surface of the teeth is more rugose than in *M. monachus* and the anterior and posterior cusps are very much less distinct, as though it is in process of losing the second posterior cusps of *M. tropicalis*. The postcanine teeth are not set obliquely.

LOWER JAW TEETH: The lower incisors are similar to those of *M. tropicalis*, the canines are small, and the postcanines are similar to those in the upper jaw.

No disease or irregularity in number is present in the teeth of either upper or lower jaws.

Skeleton

SCAPULA: The scapula of *M. schauinslandi* is very like that of *M. tropicalis*. It is similar in the way that the anterior edge is directed almost horizontally forwards from the neck before sweeping round to the dorsal surface. In *M. monachus* the anterior edge is directed forwards and upwards at an angle of approximately 45°. The spine in the young Laysan seal is represented by a low ridge with a well-developed acromion process (Fig. 4*b*).

HUMERUS, RADIUS, ULNA: No real comparison can be made because of the youth of *M. schauinslandi*, though the humerus appears to be slightly more robust than that of *M. monachus* of similar size.

MANUS: Except that the terminal phalanges are not so extensively grooved for claws as in the young *M. monachus*, although the claws themselves are of approximately similar size, the manus is not noticeably different in the three species (Fig. 4*c*).

PELVIS: The pelvis is very similar in shape to that of the young *M. monachus* although it is more mature as there is no sign of the symphysis between ischium and pubis, and the acetabulum is deep and well formed, while in the young *M. monachus* the symphysis is about half fused and the acetabulum is shallow and more obviously immature. The shape of the ischium and pubis is like that of *M. monachus* except that the pubis is possibly slightly more slender. There is no sign of the stout pubis and very narrow ischium posterior to the ischiatic spine as in *M. tropicalis*. The ilium is slightly narrower than in *M. monachus*. There is a large foramen for the obturator nerve just posterior

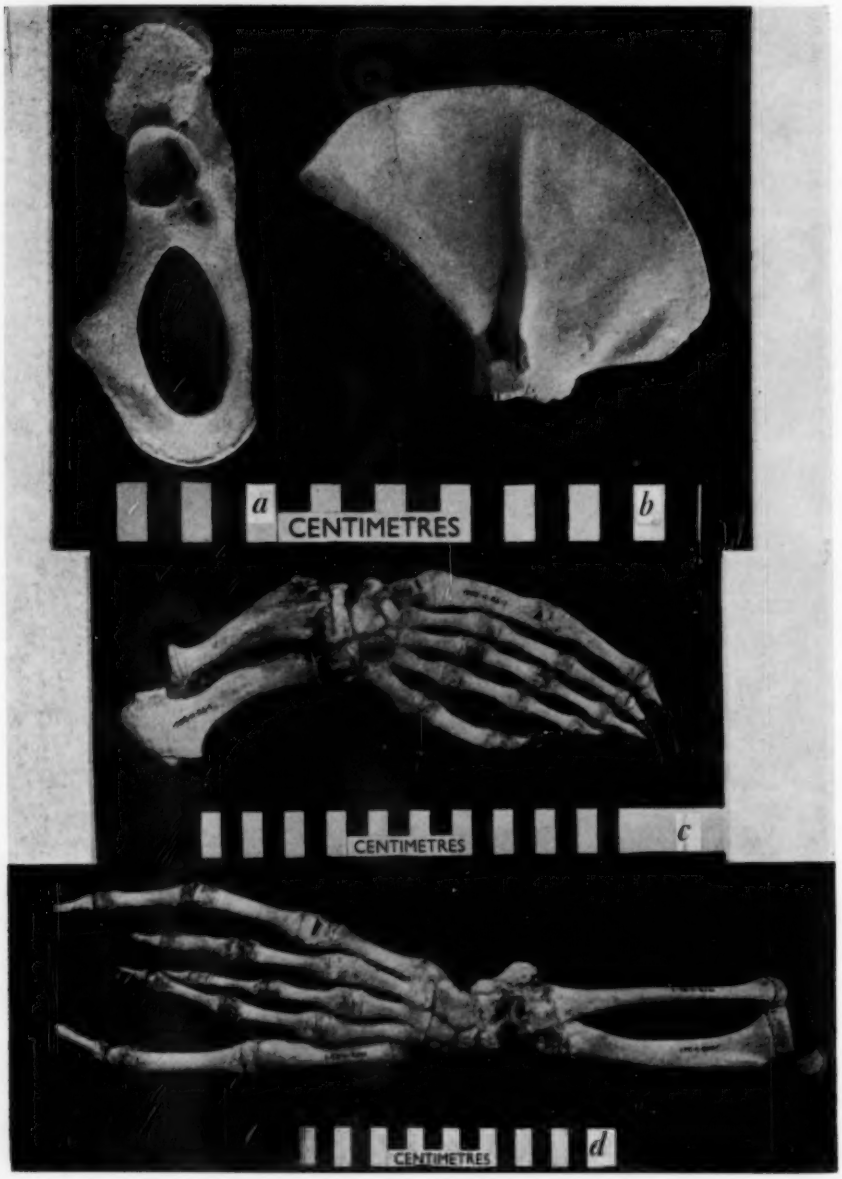

FIG. 4. *a*, Right ilium. *b*, Right scapula. *c*, Right manus. *d*, Right pes.

to the cotyloid notch that is not present in *M. monachus* or *M. tropicalis* (Fig. 4*a*).

FEMUR, TIBIA, FIBULA: These bones are not sufficiently well formed to be used for any comparison.

PES: The previous description of the pes of *M. monachus* applies also to the pes of the present animal. There is practically no indication of the insertion of the small claws on the terminal phalanges (Fig. 4*d*).

VERTEBRAL COLUMN: Vertebral formula: cervical 7, thoracic 15, lumbar 5, sacral 3, caudal 13.

Cervical vertebrae. These are more like *M. tropicalis* than *M. monachus* in that the transverse processes of vertebrae 4–6 are divided into two branches, though the division is less pronounced than in the adult *M. tropicalis*. There is a general similarity to *M. monachus*, though this is probably more because of the similarity in age. The neural arches have completely fused.

Thoracic vertebrae. These are similar to those of the young *M. monachus* except that the neural arches are narrower and do not lean so far posteriorly.

Lumbar and caudal vertebrae. These are as previously described (King, 1956).

RIBS: The articulation of the ribs is similar to that in the other monk seals. In order to inject the vascular system and remove the soft parts the cartilaginous parts of the ribs were cut away.

ABDOMINAL VEINS

The abdominal veins are thin and easily distensible. The posterior vena cava is duplicated as in *Phoca* but displays a complicated arrangement of large anastomotic channels (Fig. 5) not hitherto described in other Pinnipedia. The right limb of the posterior vena cava is the larger, is almost straight, and lies a little to the right of the midline. The smaller left limb extends from the pelvis on the left, passing somewhat obliquely cranialwards to the right to join the right limb near the upper pole of the left kidney. A large anastomotic channel passes from the right limb at the level of the lower pole of the right kidney obliquely across the midline to join the left limb at the level of the middle of the left kidney. A smaller channel arises from the right cranial end of the anastomosis just described, passes dorsal to the right limb, and enters it on the right at the level of the upper pole of the right kidney. Each limb and the two anastomotic channels receive numerous tributaries draining the renal stellate plexus as well as many vessels from the lumbar and pelvic venous plexuses. The right limb of the posterior vena cava is 2.5 cm. in diameter where it is formed by union of the iliac, lumbar, and most caudal renal tributaries. It is 3.0 cm. in diameter where it is joined by the left limb. The common trunk is 3.0 cm. in diameter throughout the 8.0 cm. of its extent to the point where it is enclosed by hepatic tissue.

The common trunk of the posterior vena cava is enlarged considerably where it enters the substance of one lobe of the multilobed liver. It has the form of a dilated tube, 15 cm. in length and 6 cm. in diameter in its cranial portion, lying on the ventral surface of the liver and surrounded on three sides by a narrow strip of hepatic tissue. Several large orifices of hepatic veins are present on the lateral walls of this dilated part of the posterior vena cava. Cranially this part of the posterior vena cava enters a hepatic sinus, nearly spherical in shape and approximately 10 cm. in diameter. The sinus is partially surrounded by hepatic tissue, but in regions only a thin translucent wall covered by peritoneum separates it from the diaphragm. The sinus is divided by two narrow septa arising from its right wall. Six large hepatic veins open into the sinus. The capacity of the sinus is estimated to be 450 cc. Figure 6 shows the appearances of the dilated vena cava and the hepatic sinus.

The intrathoracic part of the posterior vena cava is 5 cm. in length and 3.5 cm. in diameter. No pericardial plexuses of vessels, such as are found in *Phoca*, were present and no veins drained into this part of the vena cava. An incomplete sphincter of striated muscle encircles the vena cava just cranial to the diaphragm. The dorsal part of the sphincter was 3.5 cm. high and was closely adherent to the vena cava; it was separated from the diaphragmatic muscle by a narrow strip of connective tissue. The fibres of the sphincter only partially encircle the vena cava so that on its ventral aspect the sphincter is narrowed to a bundle of closely packed fibres

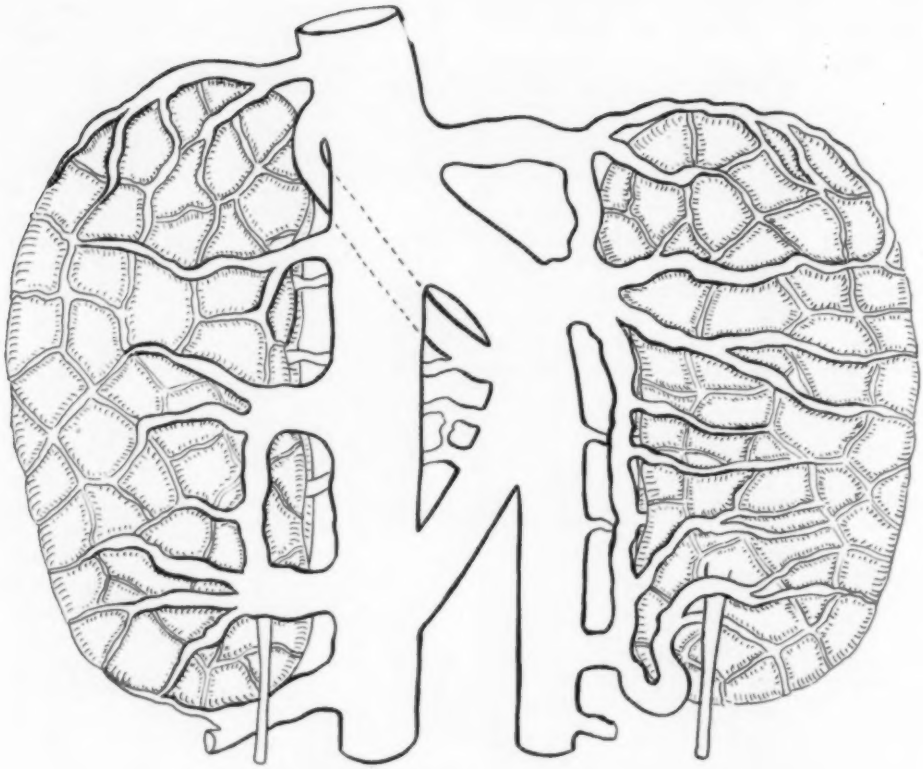

FIG. 5. A drawing from the ventral aspect to show the duplicated posterior vena cava, its anastomotic branches, and the stellate renal plexus on the surface of the multilobular kidney.

0.5 cm. high. The sphincter is shaped like a signet ring. It is supplied by branches of the right phrenic nerve.

KIDNEYS

The right kidney lies 2 cm. more cranial than the left. The right is 18 cm. long, 8 cm. broad, and 3.5 cm. thick; the left is 16 cm. long, 7 cm. broad, and 3.5 cm. thick. Each kidney is composed of large numbers of renules, each about 2.0 cm. in diameter. The papilla of each renule projects into a single calyx with a ductule that unites with others to drain eventually into the pelvis of the ureter as in *Phoca* (Harrison and Tomlinson, 1956).

Each kidney is surrounded by a stellate venous plexus, the communicating vessels of which lie in the sulci between the renules on the surface of the kidney. The plexus is more marked on the ventral aspect of the organ. There are numerous anastomoses with lumbar and lateral wall veins, with the intravertebral vein, and with the azygos vein. The plexus is drained mainly by a series of tortuous tributaries that extend round the upper and lower poles and transversely across the ventral and dorsal surfaces of the body of the kidney. These tributaries unite at the medial border of each kidney to form three or four short trunks that enter the two main limbs of the posterior vena cava or its large anastomotic

channels (Fig. 5). The major portion of venous blood is conveyed by interlobular veins reaching the surface between renules to enter the stellate plexus. Some interlobular veins, however, pass towards the hilum of the kidney to drain into small channels that extend medially to the limbs of the posterior vena cava.

HEART AND GREAT VESSELS

The aorta is markedly constricted at a point immediately to the left of the origin of the left subclavian artery and below the ductus arteriosus. This condition is known as coarctation (*coarctus* = pressed together) and is the result of partial obliteration of the dorsal aorta either between the 4th and 6th arch (above the ductus arteriosus) or below the 6th arch and the dorsal aorta (below the ductus arteriosus). It occurs rarely in man: Wood (1956) found coarctation of the aorta in 9 out of 900 cases of congenital heart disease. It appears to be very rare indeed in mammals and has not been reported in any animals dying at the Zoological Gardens, Regent's Park, London (R. W. Fiennes, personal communication). Cordy and Ribelin (1950) describe its occurrence in a bullock associated with dextraposition of the heart. It occurs, in man, more frequently in males (4.5:1), is most often found in young adults and 1 per cent of the cases have hereditary links (Wood, 1956).

FIG. 6. A drawing from the right side of a sagittal section through the dilated intrahepatic part of the posterior vena cava, the hepatic sinus, and the sphincter about the intrathoracic part of the vena cava. The hepatic sinus is divided by thin, falciform septa; the main openings of the hepatic veins are shown as black circular areas.

The transverse diameter of the monk seal aorta at the point of coarctation is 1.0 cm., that of the first part of the descending aorta is 1.4 cm. There does not appear, therefore, to be any post-stenotic dilatation of the aorta as is often found in man. The ascending aorta and its arch are dilated with marked thickening of the wall. The most dilated part is 4.5 cm. in diameter; the thickened wall is 3.0 mm. thick as opposed to the wall of the descending aorta, which is 1.0 mm. thick. At the point of coarctation the wall of the aorta is thickened by fibrous tissue to 4.0 mm. cranially and to 3.0 mm. caudally; the other parts of the aortic wall are less thick. Three aortic valves are present (only two are present in 23 per cent of human subjects with coarctation, Hamilton and Abbott, 1928). The aortic ring appears of normal size (aortic stenosis is present in 7.5 per cent of cases in man).

The left ventricular musculature appears hypertrophied, but otherwise the heart is normal. There is no patent foramen ovale and the ductus arteriosus is closed (7 per cent of human cases show a patent ductus). The right and left atria appear to be of normal size and have walls that do not look hypertrophied. There is no evidence of enlargement of vessels that provide collateral circulations above and below the constriction (internal mammary arteries). No notching of the posterior margins of the ribs (which can be caused by raised blood pressure in the intercostal vessels) is present. The lack of any such findings could well be due to the immaturity of the animal.

OTHER VEINS

A large azygos vein is present just to the right of the midline; it is 1.25 cm. in diameter and terminates in the anterior vena cava. No left-sided azygos vein is present.

An extradural intravertebral vein is present; at the level of the 12th thoracic vertebra it lies to the left of the cauda equina. At this level it measures 1.75 cm. by 1.25 cm. It is somewhat larger at the level of the 3rd thoracic vertebra. The poor preservation of the specimen prevented detailed examination of the connexions of the vein. It definitely has connexions with the azygos vein and with the lumbar veins related to the stellate renal veins at the lower poles of the kidneys as in *Phoca*. These are clearly shown after the venous system had been injected with coloured gelatin.

LUNGS

Superficial examination (no casts were made) suggests that the arrangement of the bronchial tree is symmetrical as has been described in other seals (Brown, 1958). Histological examination reveals the presence of numerous features described by Pizey (1954) in the lung of *Phoca*. The cartilages of the tertiary bronchi are continued far to the periphery of the lung, and bronchial mucous glands are frequent. The lung is divided into numerous lobules by well-marked septa of loose connective tissue. The bronchioles possess a series of myo-elastic valves which are similar to those of *Phoca* but not as marked as those in *Tursiops* (Wislocki, 1929).

TESTIS

Each testis weighs 1.9 g. and measures 25 × 15 × 10 mm. in its greatest diameters. The seminiferous tubules are inactive, immature, devoid of lumina, and average 50/μ in cross-sectioned diameter. The interstitial tissue is relatively abundant. Some of its cells are large, polyhedral, and heavily vacuolated, but the majority are small, fusiform, and have densely stained nuclei. The connective tissue between the seminiferous tubules is loosely arranged and oedematous. These appearances suggest that the gonad may well have been precociously enlarged at birth with hypertrophy of the interstitial tissue as has been described in *Halichoerus*, *Phoca*, and *Mirounga* (see Harrison, 1960, for references).

DISCUSSION

It is difficult to come to any definite conclusions from the examination of this skeleton of *Monachus schauinslandi*, not only because of the lack of comparative material but also because of the extreme youth of the animal. It is obvious that it is more closely related to *M. tropicalis* than to *M. monachus* but this is to be expected because of its geographical position. Kenyon and Rice (1959) suggest that further study may indicate a closer relationship between the Laysan and the West Indian monk seals and that *M. schauinslandi* may possibly be a race of *M. tropicalis*.

The Laysan monk seal possesses certain vascular (venous) modifications seen in other Pinnipedia. These are a duplicated posterior vena cava, a stellate renal plexus, a caval sphincter, a hepatic sinus, and an extradural intravertebral vein (Harrison and Tomlinson, 1956). There are, however, certain differences. The pattern of duplication of the posterior vena cava is more complicated than in any seal so far described. There is evidence of persistence of several anastomotic channels between the two limbs of the posterior vena cava. This could be interpreted as persistence of an embryonic state in which primitive anastomoses have become enlarged rather than suppressed. The hepatic sinus is not as large as in *Phoca* or *Mirounga*, whereas the curious dilatation of the intrahepatic part of the vena cava is undescribed in seals. The sphincter is not as large or as complete as in other Pinnipedia. It could be argued that the monk seal shows less vascular (venous) specialization than *Phoca*, *Mirounga*, *Leptonychotes*, *Lobodon*, *Halichoerus*, and *Hydrurga*, but more than *Zalophus*. This could mean that monk seals are not able to dive for so long a period or as deep as these forms. No observations have been made on the diving abilities of the Laysan monk seal, but Kenyon and Rice (1959) note that these seals occur regularly only on islands having extensive areas of shallow shoal water and that they appear to feed primarily on bottom-living fishes that they could obtain only in shallow water. They do travel over deep water, though not necessarily at any great depth. It must, however, be emphasized that the specimen described here had coarctation of the aorta. We are not

certain that its venous pattern is that prevailing in all Laysan monk seals, and it is frustrating that the first whole specimen available for examination should be congenitally abnormal.

It is hoped that continuing interest in this rare and relatively unknown seal will, in due course, result in the acquisition of more specimens for study. In the meantime it has been a great pleasure to see and work on the present animal and we are much indebted to Mr. Vernon E. Brock and his fellow workers for their kindness. We are also grateful to Dr. J. D. W. Tomlinson for injecting the specimen and for making some initial observations.

SUMMARY

A young male monk seal *Monachus schauinslandi* of an estimated age of 5 weeks has been received by the British Museum (Natural History). A brief description is given of the external features, stomach contents, and parasites. The skull and skeleton are described and a general similarity to that of *M. tropicalis* is noted. Certain modifications in the venous system are described; coarctation of the aorta is present.

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Hermaphroditic Skipjack[1]

RICHARD N. UCHIDA[2]

TWO PAIRS of skipjack (*Katsuwonus pelamis*) gonads, each having male and female components, have come to my attention in the past 3 years. The first was received from Mr. Thomas S. Higa, proprietor of a Honolulu fish retail market, in April 1957. Mr. Higa recovered the gonads from a neighboring fish retailer who had discovered them in a freshly eviscerated 16-lb. skipjack. This fish was captured by the "Orion," a commercial skipjack vessel, on April 11, 1957, off Makua, Oahu, from a school of 15- to 18-lb. skipjack.

The ovo-testes (Fig. 1) were typically paired and elongate, joined posteriorly, and weighed 121 gm. (fresh weight). The male and female components were easily discernible. The left gonad was divided into three segments; the anterior one-sixth and posterior one-third were ovarian and the remainder testicular. The right gonad was divided into two segments; about two-thirds of the anterior portion was testicular and the remainder ovarian. Figure 2 shows the length of each of these segments.

The cream-colored testicular sections were solid and somewhat flattened in cross-section, and did not seem to be atypical in any way. There was no running milt present, but their size suggested that they were in a rather advanced stage of maturity. All ovarian sections were pinkish, but differed in firmness. The posterior segments were hollow and flabby, with a ribbed internal cavity extending their entire length. The single anterior ovarian section was nearly round in cross-section and rather turgid.

Detailed examination of the ovo-testes was made after they had been preserved in 10 per cent formalin. The longitudinal duct of each testicular section could be followed posteriorly to the juncture of the testicular and ovarian segments, after which the ductus deferens became obscured in the network of blood vessels on the surface of the ovarian section. No openings of the ductus deferens were detected anywhere in the area of the urogenital sinus.

The two posterior ovarian sections were joined posteriorly by a single oviduct which opened into the urogenital orifice. No duct could be found in the single anterior ovarian segment.

Microscopic examination of the ova was made to determine their degree of maturity. The lumen of the anterior ovarian section was filled

FIG. 1. The ovo-testes of a hermaphroditic skipjack (ventral view).

[1] Published with permission of the Director, U. S. Bureau of Commercial Fisheries. Manuscript received July 29, 1960.

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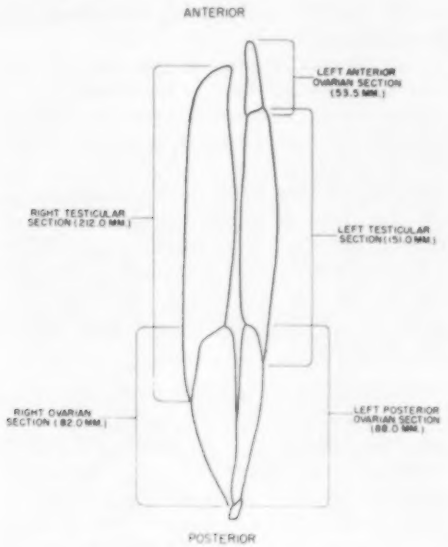
ANTERIOR
LEFT ANTERIOR OVARIAN SECTION (53.5 MM.)
RIGHT TESTICULAR SECTION (212.0 MM.)
LEFT TESTICULAR SECTION (151.0 MM.)
RIGHT OVARIAN SECTION (82.0 MM.)
LEFT POSTERIOR OVARIAN SECTION (88.0 MM.)
POSTERIOR

FIG. 2. Outline of the ovo-testes, showing the location and size of the male and female components (ventral view).

with a compact mass of resorbing ova, while the peripheral portion contained ova ranging from small, transparent stages to larger, opaque ova. The average diameter of 25 randomly selected larger, opaque ova was 0.504 mm. The posterior ovarian sections contained similar small and large ova, but no resorbing ova were present. Average diameters of randomly selected ova from these parts were 0.543 mm. for the left posterior member and 0.514 mm. for the right.

The presence of residual ova in the anterior section suggests that the fish had been a functional female. Assuming that the ova in each of the ovarian sections ripened at the same time, it is possible that ova were extruded from the posterior sections at spawning time, whereas ova in the anterior section could not be extruded because of the lack of an adequate duct. This could account for the presence of the resorbing ova in the lumen of the anterior ovarian section. Since the testicular sections were well developed and constituted a large part of the gonads, the fish may also have been a functional male.

The discovery of the second pair of ovo-testes was reported to the Honolulu Biological Laboratory on March 10, 1960, by Mr. Richard Nakashima of Honolulu, who found them in a 10-lb. skipjack.

The gonads, outlined in Figure 3 and labeled *A* and *B* for purpose of identification, were not joined posteriorly as a result of mutilation to both posterior ends during removal, and, therefore, could not be identified as to position (left or right). Both gonads were distinctly separated into three parts; an anterior ovarian section, a middle testicular portion, and a torn, fragmentary ovarian segment posteriorly. The testicular segments were similar to those found in the ovo-testes previously described, and contained no running milt. The ovarian sections were predominantly yellow with a tinge of pink. The anterior segments were flabby and hollow.

A starch suspension colored with powdered carmine was injected into the posterior ovarian section of gonad *A* and the flow of injected material indicated the presence of a duct connecting the two ovarian parts. A similar injection was attempted with gonad *B*, but failed

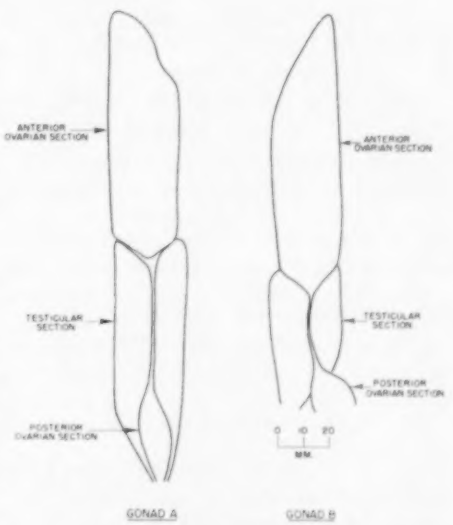

FIG. 3. Outline of the ovo-testes, showing the location and relative size of the male and female components.

to reveal any ducts owing to excessive tissue damage.

Ova diameter measurements revealed that the posterior ovarian section of gonad *A* and both ovarian segments of gonad *B* were identical in their degree of development. The ova ranged from small, primitive ova to larger, opaque ova. Average diameters of 25 randomly selected ova of the most advanced group were 0.479 mm. for the posterior ovarian section of gonad *A* and 0.476 mm. and 0.479 mm. for the anterior and posterior ovarian sections, respectively, of gonad *B*.

The development of the anterior ovarian section of gonad *A* was dissimilar to any of the sections previously examined. Its lumen contained a loose mass of large, ripe, resorbing ova, together with a few completely degenerated ova. The peripheral portion of the section contained only primitive ova. Those intermediate to the primitive and the large, resorbing ova were absent.

The presence of residual ova indicates that this fish also had been a functional female. Again, it is not clear whether the ova remnants were the unexpelled portions of a previous successful spawning or a group of ripe ova that were not expelled owing to the inadequacy of the duct. Damage to the posterior portions of both gonads made it impossible to determine whether the male ducts were connected to the exterior, but since the testicular segments were well developed, this fish may also have been a functional male.

Hermaphroditism in skipjack is an extremely rare occurrence. So far as is known, only one other example has been recorded and described (Nakamura, H., 1935, Trans. Nat. Hist. Soc. Formosa 25(141): 197–198; in Japanese).

Studies on Pacific Ferns, Part IV
The Pteridophyte Flora of Pitcairn Island

G. BROWNLIE[1]

ALTHOUGH THE FERNS of southeastern Polynesia have been described in several papers, no separate list has previously been provided for Pitcairn Island. The present paper outlines the details of a collection made there by Mr. W. H. Lintott of the Botany Department of the University of Canterbury, and includes mention of other collections where these were available. When the changes which have occurred in the indigenous vegetation are considered, it is remarkable that, as well as finding all the other species noted earlier, one species not previously recorded from Pitcairn is included in the most recent collection.

Of the 20 species listed, 15 are widespread throughout Polynesia, and 2 others are probably local derivatives of similarly widespread species. This large group represents the dominant Malay-Papuan element found in decreasing numbers of species from west to east in the tropical Pacific. Of the remaining 3, 1 species of *Asplenium* and 1 of *Trichomanes* are found in S.E. Polynesia and New Zealand, and are the only ones to which Copeland's (1938) ideas of an Austral group can be applied. The single species of *Cyathea* is related to ferns found in Rapa and the Society Islands. There are only 2 species recognised as endemics, and each of these may in fact be better regarded as varieties. Viewed as a whole, the pteridophyte flora of this region, Pitcairn, Rapa, and the Australs, appears to be merely an extension of that of the Society Islands.

Abbreviations: C, Department of Botany, University of Canterbury; W, Dominion Museum, Wellington; S, Department of Agriculture, Suva, Fiji; K, The Herbarium, Royal Botanic Gardens, Kew.

[1] Department of Botany, University of Canterbury, Christchurch, New Zealand. Manuscript received April 25, 1960.

PSILOTACEAE

Psilotum nudum (L.) Grisebach

Pendant on trees and shady rocks; not common. Widely distributed throughout Polynesia.

Lintott 167a and 167b (C), Williams 3068 (W), Twyford S.P. 129 (S).

MARATTIACEAE

Angiopteris chauliodonta Copeland

On damp hillsides in dense shade. I doubtfully retain this as a distinct species, and it may be only a local form in which the sterile apices of the pinnules are more toothed than is usual in *A. evecta*.

Lintott 150 (C), Twyford S.P. 130 (S).

GLEICHENIACEAE

Dicranopteris linearis (Burm.) Und.

Gleichenia linearis (Burm.) Clark. Brown, B.P. Bishop Mus. Bull. 89, 97, 1931.

Copeland, Occ. Pap. B.P. Bishop Mus. 14(5): 52, 1938.

Forming tangled masses on dry hillsides. Widely distributed in the tropics and subtropics of the Old World with many recognized varieties in S.E. Asia. It is probable that there are also several varieties in the Pacific area, but these have not been worked out.

Lintott 163, 164 (C), Twyford S.P. 135 (S), Williams 3038, 3081 (W), Fosberg 11221 (K), Quayle No. X (K).

HYMENOPHYLLACEAE

Trichomanes endlicherianum Pr.

Damp rocky faces in shady stream bed. This is the only record of a member of this family from Pitcairn, and as it appears to be fairly uncommon, it has presumably been overlooked by previous collectors. The specimens are some-

what smaller than those from the Austral Islands and New Zealand, but they have the characteristic single row of elongated marginal cells. The species is found in New Zealand, the Kermadecs, Samoa, Fiji, Tahiti, the Australs, and Rapa.

Lintott 155 (C).

PTERIDACEAE

Adiantum hispidulum Sw.

In isolated clumps on dry slopes and in rocky crevices. All examples are considerably smaller than those seen from the larger Pacific islands. The species is widely distributed in the tropics and subtropics from Africa to Polynesia and south to New Zealand.

Lintott 152, 152b (C), Twyford S.P. 51 (S), St. John 15031 (K).

CYATHEACEAE

Cyathea cumingii Bak.

Tree fern up to 10 ft. high, occurring in several places on the island. Elsewhere known only from the Australs, but *C. rapensis* and *C. societarum* are very similar, if not identical.

Lintott 165 (C), Williams 3010, 3011 (W), Twyford S.P. 132 (S), Quayle No. 1 (K), Cuming 1393 (K), Matthews No. 7 (K), Fosberg 11241 (K), St. John 14978 (K).

DAVALLIACEAE

Davallia solida (Forst.) Sw.

Common everywhere, creeping on the ground and as an epiphyte on old trees. Four local forms have been recognized in S.E. Polynesia by Brown (1931), but the species is everywhere somewhat variable in degree of division of the fronds and in shape of the indusia. It is distributed from Burma to Pitcairn.

Lintott 162 (C), Williams 3013, 3052 (W), Twyford S.P. 133, 134 (S), Quayle No. X (K), St. John 15048 (K).

Nephrolepis biserrata (Sw.) Schott

Common throughout the island underneath *Pandanus*. Christensen (1943) regards the Polynesian-Asiatic forms as probably distinct from genuine African *N. biserrata*, but until a complete revision of the genus has been carried out it is preferable to retain the well-known name. The distribution of the species in its widest sense is pantropic.

Lintott 158 (C), Williams 3074, 3079 (W), Twyford S.P. 59(S), Quayle No. 1 (K).

Nephrolepis hirsutula (Forst.) Pr.

Fairly common, particularly around clearings. Very variable in all its characters, often approaching close to *N. biserrata*, although it is usually smaller than that species. Distributed from tropical Asia to Pitcairn.

Lintott 169 (C), Williams 3051, 3078 (W), Twyford S.P. 136 (S).

ASPIDIACEAE

Thelypteris uliginosa (Kze.) Ching

Dryopteris setigera (Bl.) Kze. Brown, B.P. Bishop Mus. Bull. 89, 30, 1931.

On cleared banks along shady tracks. I have seen no fertile specimens of this fern from Pitcairn, and it appears to be relatively uncommon. The species is widespread in the tropics and subtropics from Asia through the Pacific to Pitcairn.

Lintott 168 (C), Twyford S.P. 131 (S).

Rumohra aristata (Forst.) Ching

Polystichum aristatum (Forst.) Pr. Brown, B.P. Bishop Mus. Bull. 89, 38, 1931.

Copeland, Occ. Pap. B.P. Bishop Mus. 14(5): 57, 1938.

Forming small patches under trees on hillside ridge of Adamstown. Brown was in error in comparing specimens of this fern from Rapa with New Zealand forms, for, although found in the Kermadecs, it does not occur on the mainland of New Zealand. Distribution is throughout the tropics and subtropics of the Old World.

Lintott 154 (C), Quayle No. X (K), St. John 14969 (K).

Cyclosorus parasiticus (L.) Farwell

Dryopteris parasitica (L.) Kze. Brown, B.P. Bishop Mus. Bull. 89, 22, 1931.

Dryopteris dentata (Forst.) C. Chr. Copeland, Occ. Pap. B.P. Bishop Mus. 14(5): 56, 1938.

Common everywhere in shady positions. The habit of these specimens is almost intermediate between typical *C. parasiticus* and *C. nymphalis*, but since the leaves are not fascicled it is better to place it in the former species. I feel that Brown's recognition of a local variety based chiefly on characters of size is, however, unsound. Widely distributed from tropical Asia through the Pacific.

Lintott 156 (C), Williams 3049, 3076 (W), Twyford S.P. 100 (S).

Athyrium polyanthes (Sol. ex Bak.) Copel.

Diplazium polyanthos (Sol.) C. Chr. Brown, B.P. Bishop Mus. Bull, 89, 55, 1931.

Athyrium pitcairnense Copel., Occ. Pap. B.P. Bishop Mus. 14(5): 60, 1938.

Diplazium harpeodes Moore. C. Chr., B.P. Bishop Mus. Bull. 177, 76, 1943.

Not common; found in isolated clumps in shady valleys. Much of the confusion concerning the nomenclature of this species was cleared up by Christensen (1943), but I prefer to follow Copeland in uniting *Diplazium* and *Athyrium*. Copeland's local species falls within the range of the species as outlined by Christensen. Distribution is throughout the Pacific islands from Fiji to Pitcairn.

Lintott 166 (C), Cuming 1389 (K), Matthews unnumbered (K).

BLECHNACEAE

Doodia media R. Br.

Fairly common on open ground and underneath *Pandanus*. Distributed from Australia and New Zealand to Pitcairn, but absent from Samoa and Tahiti.

Lintott 159a and 159b (C), Williams 3044 (W), Twyford S.P. 133, 134 (S), St. John 14976 (K).

ASPLENIACEAE

Asplenium nidus L.

Common in one or two valleys and cultivated in local gardens. Widely spread throughout the tropics of the Old World.

Lintott 153 (C).

Asplenium obtusatum Forst.

On rocks on the south coast, and in small caves. Always within or close to the spray zone. The specimens are similar to those found on Rapa, the Australs, and other Pacific islands, but are somewhat smaller than the typical state represented in New Zealand. Elsewhere the species is found in Juan Fernandez and southern Chile, with closely related, if not identical, species on Tristan da Cunha and Tasmania.

Lintott 170 (C), Williams 3083 (W), Twyford S.P. 71, 73 (S), Fosberg 11343 (K).

Loxoscaphe gibberosum (Forst.) Moore

Loxoscaphe gibberosum var. *pitcairnense* Brown, B.P. Bishop Mus. Bull. 89, 67, 1931.

Common everywhere in deep shade. This species shows so much variation in the degree to which the leaf segments extend beyond the sorus that I feel that Brown's varieties are difficult to maintain. It is found in the Pacific region from Fiji to Pitcairn, but is absent from Samoa.

Lintott 157 (C), Williams 3012, 3053 (W), Twyford S.P. 43 (S), Matthews unnumbered (K), Cuming 1373 (K), Fosberg 11297 (K).

POLYPODIACEAE

Pyrrosia angustata (Sw.) Ching

Cyclophorus angustatus (Sw.) Desv. Brown, B. P. Bishop Mus. Bull. 89, 93, 1931.

Common on rocks in inland situations, and as an epiphyte on large trees. The species is

widely distributed in tropical areas from Malaya to Polynesia.

Lintott 161a, 161b (C), Williams 2997, 3075, 3082 (W), Twyford S.P. 153 (S), Matthews unnumbered (K), Cuming 1394 (K).

Phymatodes pitcairnense (Copel.) Brownlie, comb. nov.

Polypodium phymatodes L. Brown, B.P. Bishop Mus. Bull. 89, 87, 1931 (in part).

Microsorium pitcairnense Copel. Occ. Pap. B.P. Bishop Mus. 14(5): 74, 1938.

Common, creeping on banks along paths. This is a close relative of *P. nigrescens*, but without the distinct veins of that species. Unlike Copeland, I do not find that the sori of any of the specimens are relatively marginal, so that these may not be the same as his species. However, until a full revision of the Pacific members of this genus is undertaken, I feel that it is unwise to introduce further new names for minor differences.

Lintott 160 (C), Williams 3067, 3077, 3084 (W), Twyford S.P. 36, 65 (S), Matthews No. 12 (K).

VITTARIACEAE

Vittaria elongata Sw.

Local, in one area growing on moist rocks. The limitations of this species are somewhat uncertain in the Pacific area, and the Pitcairn example is doubtfully assigned to it. It may in fact be closer to *V. rigida* var. *samoensis* described by Christensen (1943). In the widest sense the species extends from tropical Asia to Polynesia.

Lintott 151 (C), Fosberg 11309 (K).

In addition to the above-listed species there are two sheets at Kew (Cuming 1388) identified as *Polypodium sandwicense*. The specimens belong to the genus *Ctenitis* and approach close to *Dryopteris samoensis* (C. Chr. 1943), but the fact that it has not been found by any subsequent collector indicates that it is probably extinct on Pitcairn or has been wrongly accredited to that island.

I wish to thank the professors W. R. Philipson and Harold St. John for making the Lintott collection available for study, and I wish to acknowledge the use of material from the Dominion Museum, Wellington, the Department of Agriculture, Suva, and the Herbarium, Royal Botanic Gardens, Kew.

The Principal Weedy Melastomaceae in Hawaii

D. L. PLUCKNETT and B. C. STONE[1]

NONE OF THE NUMEROUS SPECIES of Melastomaceae is native to the Hawaiian Islands, yet at present at least a dozen species in nine different genera are found as weeds or seminaturalized plants in various localities in the Islands. Some of these species are hardly known out of cultivation, others are frequent in certain small areas, while a few are well-known common plants on most of the islands in the chain. Certain areas have become thickly populated with one or another of these species, and waste and pasture areas have been invaded, becoming in some cases nearly impenetrable thickets. Two or three of these species must be regarded as noxious weeds.

In Hillebrand's *Flora of the Hawaiian Islands* (1888) there is no mention of any melastomaceous species. Degener (1935: family 274) mentions *Heterocentron*, and (1930: 226) mentions *Tibouchina semidecandra* and *Melastoma malabathricum*. Earlier, W. T. Pope (1929: 147) had mentioned *Melastoma decemfidum* and stated that it had escaped from cultivation on Kauai, and had been introduced (presumably from a Florida nursery) in 1916. It seems from recent collections that this plant mentioned by Pope is, as Degener indicated, *M. malabathricum;* although both species are present in the Islands, only this one has been found on Kauai. The *Tibouchina* is said to have been introduced to Hawaii in 1910.

Degener indicated the pestiferous nature of these plants, and his prediction that they would spread has come true. At present they have a very spotty distribution, but where they have spread they often form virtually pure stands which have blighted many areas of natural vegetation and have become a foe of both the agriculturist and conservationist. Hosaka (1945) referred to *Melastoma malabathricum* as "an aggressive shrub that forms dense stands—crowds out other plants . . . has no forage value."

Recently the extent of bauxitic or aluminous soils in Hawaii has been publicized (Sherman, 1954), and plants which accumulate aluminum have been the subject of a paper by Moomaw, Nakamura, and Sherman (1959). Among the Hawaiian plants found to accumulate aluminum was *M. malabathricum*, a known accumulator of aluminum in other areas (Webb, 1954). None of the other melastomaceous plants in Hawaii was used in the study by Moomaw *et al.*, but other species of the Melastomaceae are reported by Webb to accumulate aluminum.

The purpose of this paper is to discuss the distribution and spread of the noxious Melastomaceae in Hawaii with special reference to the most common species and to provide a key and brief descriptions of each as a preliminary step for a possible study of bauxitic soils and aluminum-accumulating species of Melastomaceae.

Three species are found on more than one island and may be considered common. These are *Tibouchina semidecandra, Melastoma decemfidum,* and *M. malabathricum.*

Three other species are rather abundant in a few isolated locations on one or two islands. These are *Clidemia hirta, Pterolepis glomerata,* and *Heterocentron subtriplinervium.*

The remaining species are restricted to a few small areas and do not threaten to become noxious weeds. These are *Oxyspora paniculata, Arthrostemma latifolium, Tetrazygia bicolor,* and *Medinilla magnifica.* Some of these species are referred to by Neal (1948: 569).

KEY TO COMMON SPECIES

Petals and all anthers brilliant purple; leaves densely silvery-pubescent with soft hairs, especially on undersides; open shrubs up to 12–15 ft. tall....*Tibouchina semidecandra* (1)

Petals pink, stamens pink or yellow; leaves

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pubescent but not densely silvery; with stiff hairs; compact shrubs usually 10 ft. tall or less.

1. Petioles and nodes set with sparse long stiff hairs up to 5 mm. long; calyces rather sparsely scaly; ribs below sparsely scaly; lateral veins more or less glabrous..... .....*Melastoma decemfidum* (2)
2. Petioles and stems set with numerous short spinules to 1 mm. long; nodes with a few long scales; calyces silky with numerous scales; ribs and small veinlets rather densely scaly-spiny below .....*Melastoma malabathricum* (3)

1. *Tibouchina semidecandra* (Schrank and Mart.) Cogniaux

DISTRIBUTION: *Kauai:* Kokee, open grass area by museum, on ditch bank by roadside, Dec. 23, 1959, D. L. Plucknett 81–85.

Hawaii: N.W. Kilauea Crater, wet fern forest around houses, 1150 m., Aug. 30, 1933, Fosberg 10121. Volcano Road, near volcano, forest reserve along road, in mixed fern forest, tall shrub 5 m. high, Nov. 10, 1926, L. H. Mac Daniels 223. Volcano House, July 24, 1926, Aug. 24, 1926, C. S. Judd. 29 miles, Glenwood, Hawaii, July 23, 1926, Degener 8188; June 22, 1929, persistent in forested region, Degener 9641. Glenwood, el. 1000 m., in forest, Dec. 25, 1930, E. H. Bryan, Jr., 714. Kalanilehua, Aug., 1917, J. F. Rock 13029, 13030. Kurtistown, Jan. 20, 1960, along roadside, D. L. Plucknett 95. Hilo, May, 1932, A. Meebold.

Oahu: Nuuanu Valley, upper part near Upside Down Falls, well established in underbrush in thick woods, shrub 2 m. tall, flowers deep purple, Fosberg 27067, Sept. 15, 1946. Tantalus, grounds of E. F. Bishop, Oct. 3, 1930, H. E. Gregory. Observed, Manoa Valley, by Manoa stream, B. C. Stone, Feb. 1960.

Altitude range 1,500–4,500 ft.; requires moist relatively cool habitat. At lower elevations it is usually under shade, but at Kilauea Crater it may be found in the open (elev. 3,400 ft.). This species is a spectacular shrub and in cultivation is very attractive. It does not appear to be as aggressive as the two *Melastoma* spp. and tends to spread only in disturbed areas. It has not been found deeply penetrating the native forest, but is often very common along roadcuts, houselots, trails, and near buildings.

2. *Melastoma malabathricum* L.

DISTRIBUTION: *Kauai:* Kilohana Crater, dominant shrub, 320 m., 7 Aug. 1928, E. H. Bryan 626. Reservoir near Hanahanapuni Crater, Mar. 24, 1960, Plucknett 116, 117. Wailua bauxite project area, Mar. 24, 1960, Plucknett 118–123.

Hawaii: Anauulu Rd. above Hilo, side of gully in canefield, flowers pink, Dec. 7, 1933, alt. 400 m., Fosberg 10490. Kaumana, alt. 200 ft., flowers pink, Sept. 1953, Amy Suehiro. Keaau Orchard–Volcano Highway Intersection, by roadside, Dec. 4, 1959, Plucknett 78. Hilo–Volcano Road, 4 miles mauka, Jan. 20, 1960, roadside, Plucknett 93, 94. Hilo radio tower, Jan. 20, 1960, Plucknett 89, 90, 92.

Altitude range 0–1,000 ft. In contrast to *Tibouchina, Melastoma malabathricum* is tolerant of drier and warmer habitats and tends to spread in lowland areas rather than in disturbed areas of native forest. Usually found in open habitats such as pastures, waste areas, and fields with weedy vegetation. On Kilohana Crater on Kauai and the adjoining areas where it once was dominant, *Rhodomyrtus tomentosa* (Ait.) Hassk. appears now to be replacing it, but it still remains an important weedy species in this area.

Pope's reference (1929: 147) to *Melastoma decemfidum* on Kauai is probably in error since only *M. malabathricum* has been found on that island. The plant is known on Kauai as "Isenberg bush" probably because of its association with Kilohana Crater and the Isenberg home there. *Rhodomyrtus tomentosa* has also been called "Isenberg bush" on Kauai but it more commonly is known as "Indian gooseberry."

On Hawaii *Melastoma malabathricum* may be found in great abundance in the Keaukaha area near the Hilo Airport and along the Volcano Road.

M. malabathricum is vigorous in growth and spreads rapidly from numerous seeds, usually spread by birds.

3. *Melastoma decemfidum* Roxb.

DISTRIBUTION: *Hawaii:* Hilo, sent to J. Kim, Honolulu, B. Ag. Forestry, 10 Dec. 1957. Hilo–

Volcano Road, 4 miles above Hilo, top of road cut, Dec. 5, 1959, Plucknett 79, 80.

Altitude range 0–1,000 ft. Flourishes in open areas of high rainfall on Hawaii. Together with its weedy relative, *M. malabathricum*, *M. decemfidum* has become dominant in the Keaukaha area near the radio tower and also may be seen in thickets along the Volcano Road. This shrub has been observed as a small tree with a trunk 4–5 in. in diameter and up to 12 ft. high in the Keaukaha area.

LESS COMMON MELASTOMACEOUS PLANTS IN HAWAII

There are several species which seem to be spreading in certain areas but which at present cannot be classed as dangerous or even common weeds. It seems useful to indicate briefly their presently known distributions.

Clidemia hirta (L.) D. Don. This rather small plant has been collected on Oahu on Mt. Tantalus, twice on the Poamoho Trail in the Koolau range, and twice near the Hawaiian Sugar Planters' Association nursery in Wahiawa. There are no reports of *Clidemia* from the other islands.

Pterolepis glomerata (Rottb.) Miquel. Specimens of this plant have been collected from Palikea in the Waianae range, and from Poamoho and Pupukea in the Koolau range on Oahu.

Heterocentron subtriplinervium (Link and Otto) Br. and Bouche. According to the labeled specimens in Bishop Museum there are four species of *Heterocentron* in Hawaii, but probably only one or two of these species are actually represented. Neal (1948: 568) reported only *H. roseum* Br. and Bouche. Clarification of the species of *Heterocentron* will probably be presented in the new edition of Neal's *In Gardens of Hawaii* (in preparation).

There are five specimens determined as *H. subtriplinervium* in the Bishop Museum. These were collected from Mt. Tantalus, Oahu, and from Hawaii along the Hilo–Kona and Hilo–Kilauea roads.

Arthrostemma latifolium D. Don. This plant has been found escaping at the Makiki Nursery, in Honolulu, and along south Opaeula ridge on Oahu.

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Leaf and Air Temperature under Hawaii Conditions

T. L. NOFFSINGER[1]

AIR TEMPERATURE may give a poor indication of the actual temperature experienced by a plant leaf under various meteorological conditions. Leaf temperature is dependent upon the type and condition of the plant as well as on a number of meteorological elements including wind, humidity, cloud cover, solar radiation, and air temperature.

MATERIALS AND METHODS

During the period from March 9 through April 15, 1960, leaf and air temperatures were measured using a 12-channel single-input thermister-type thermometer. Leaf temperatures of pineapple and papaya plants were measured using a 22-gauge hypodermic probe. Air temperature was measured with the thermister air temperature probe and checked with a standard mercury-in-glass thermometer. The wet-bulb temperature was determined by a standard psychrometer and solar radiation was measured by a recording bimetallic actinograph (pyrheliometer).

Soil temperature was measured from a mercury-in-glass thermometer implanted ¼ in. in the soil.

In measuring leaf temperatures the needle was carefully inserted from the underside of the leaf, parallel to the leaf veins, to approximately ½ in.; i.e., at least ½ in. of the probe was enclosed within the leaf tissue. All temperatures were read to the nearest 0.1° C. The average temperature of the plant was taken as the mean value obtained from one leaf exposed to solar radiation and one in shade.

RESULTS

Data were collected at 0800, 1200, and 1600 hr. during the period of March 9 through April 15. In addition, a continuous hourly collection was made over a 24-hr. period from 0800, April 11, through 0700, April 12.

During the daylight hours pineapple leaf temperature was consistently higher than the air temperature measured in an instrument shelter at the same elevation as the plants. The values usually ranged from 1.5° to 3.5° C. above the air temperature but occasionally a leaf exposed to direct sunlight had a temperature as much as 7.6° C. higher than the air temperature.

The corresponding average temperature of the papaya leaf was consistently lower than the air temperature. Temperature of leaves exposed to direct solar radiation and temperature of leaves on the same plant but shaded by higher leaves are given in Table 1 together with the average air temperature, average leaf temperature, soil temperature, and solar radiation values.

Table 2 gives air temperature, leaf temperature, insolation values, soil temperature, cloud cover, and wind speed at 4-hr. intervals for a 24-hr. period April 11 through April 12. Maximum air temperature (27.0° C.) occurred at 1300; maximum soil temperature for the pineapple (28.0° C.) occurred at 1400; maximum soil temperature for the papaya (30.5° C.) occurred at 1500 and 1600. Maximum average leaf

TABLE 1

LEAF AND AIR TEMPERATURE AND RELATED METEOROLOGICAL DATA FOR MARCH 9–APRIL 15, 1960

TIME	0800	1200	1600
Air temperature °C.	21.5	26.7	26.4
Leaf temperature °C.			
Pineapple			
average	23.2	29.1	26.6
in sun	24.7	31.0	28.0
in shade	21.7	27.2	25.2
Papaya			
average	21.3	25.4	24.5
in sun	21.7	25.9	24.9
in shade	20.9	24.9	24.1
Insolation Langleys/min.	0.21	0.99	0.74
Soil temperature			
Pineapple	19.5	26.4	26.3
Papaya	19.5	27.1	29.8

[1] Climatologist, Land Study Bureau, University of Hawaii. Manuscript received May 19, 1960.

TABLE 2

LEAF AND AIR TEMPERATURE AND RELATED METEOROLOGICAL DATA FOR 0800 APRIL 11–0800 APRIL 12, 1960

TIME	0800	1200	1600	2000	2400	0400	SUNRISE
Air temperature °C.	22.0	25.7	26.7	22.3	22.2	21.9	22.0
Leaf temperature °C.							
Pineapple							
average	23.5	29.5	27.1	21.7	21.5	22.1	21.7
in sun	25.0	31.5	29.0	.....	.....	.....	.....
in shade	21.9	27.5	25.1	21.7	21.5	22.1	21.7
Papaya							
average	21.3	25.1	24.8	21.2	20.5	21.0	21.7
in sun	21.6	25.0	26.0	.....	.....	.....	.....
in shade	21.0	25.1	23.5	21.2	20.5	21.0	21.7
Insolation							
Langleys/min.	0.27	1.43	0.98	.....	.....	.....	.....
Soil temperature							
Pineapple	20.2	26.5	27.0	23.7	21.4	21.4	20.5
Papaya	20.5	27.0	30.5	24.2	21.2	21.2	20.5
Cloud cover (1/8 S.)	5	6	1	1	1	5	1
Wind (knots)	8	8	10	5	4	0	0

temperature in the pineapple plant (29.6° C.) occurred at 1500 and in the papaya plant (26.8° C.) at 1300.

DISCUSSION

Plants undergo irradiation from the sun, clouds, and sky during the daylight hours, and at night they radiate heat outward. Mäde (Geiger, 1950: 278–280) kept a continuous record of leaf temperature over a period of two days and found that during the middle of the day the leaf surface of *Bilbergia nutaus* (a hothouse plant of the pineapple family) was as much as 10° C. higher than the air temperature. The interior portion of the pineapple fruit exposed to the direct rays of the sun at latitude 21° N. may experience temperature from 5° to 8° C. above the free air temperature. In Formosa it has become a practice to shade the pineapple fruit in order to prevent heat damage from solar radiation (Ekern, personal communication). Waggoner and Shaw (1952) have shown that energy losses from potato and tomato plants at night due to transpiration may be very small. Geiger (1950: 276) states that plant temperature is generally higher than that of air temperature when the ground surface is warmer than the air layer resting upon it, and that by night the plant is, for the most part, cooler than the air. An examination of air, soil, and leaf temperatures in Tables 1 and 2 shows that the generalization made by Geiger holds for pineapple, but that the average leaf temperatures of the papaya were consistently lower than the air temperature even during periods of relatively high soil temperature. In one observation during the period (not shown in the table), the temperature of the papaya leaf exposed to the sun registered 2.6° C. higher than the air temperature. At that time the value for solar radiation was 1.42 calories per sq. cm. per min., the sky was five-eighths covered with cumulus and stratocumulus clouds and a light sprinkle of rain was falling from clouds immediately to the N.E. of the station.

SUMMARY

Air temperature in an instrument shelter at the level of the plants does not provide a good measure of plant temperature. Papaya, with a respiration and transpiration pattern characteristic of the mesophytes, shows a leaf temperature which remains relatively near the air temperature but may be higher or lower than the air temperature, depending upon the condition of radiation, cloud cover, and wind. Pineapple, a xerophyte, has leaf temperature during the daylight hours which average 1.5° to 3.5° C. above

the air temperature, and for short periods of high solar radiation a leaf temperature 7.6° C. above the air temperature was recorded. Generally, leaf temperatures of both pineapple and papaya were below the air temperature during the night except for one period in which clouds moved into the area. At 0400, April 12, with five-eighths cloud cover and calm wind, the temperature of the pineapple leaf rose to 0.3° C. above the air temperature.

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NOTE

The Species Commonality Index: A Method for Comparing Habitats

Ecologists have used a variety of methods for comparing habitats in order to point up their similarity and to predict the efficacy of transplants. Some methods are based upon what are believed to be outstanding physical differences and similarities between the habitats, while others are based upon faunal and floral similarities and differences. The following is a method based upon faunistic similarity.

For 3 years the writer has used a simple technique involving the number of species in common between two habitats in order to arrive at a single value for comparison. This number, the Species Commonality Index (SCI), is arrived at by dividing the number of species common to both habitats by the total number of species present, as shown in the following example.

HABITAT I	HABITAT II
Species Present	*Species Present*
A	A
B	B
C	C
L	L
M	N
O	P
R	Q
S	U
T	V
	W

$$\text{Species in Common} = 4$$

$$\text{Total Number of Species} = 15$$

$$\text{Species Commonality Index} = \frac{4}{15} = .27$$

In order to make even semivalid comparisons using this technique, the collections should be thorough and reasonably concurrent. The writer has found that a large group of interested students (for example a group of young biology majors), make very comprehensive collections. The following data were compiled by 30 students in an elementary ecology class at Western Washington College of Education during the months of March and April, 1960, and show to what purpose the SCI might be used.

From inspection of the data shown in Table 1, it is apparent that Whatcom Rapids and Bad Pond are least similar. One would expect a rapids area to bear little faunistic similarity to a pond habitat, and thus it is seen that whenever Whatcom Rapids is compared to a pond, the SCI is relatively quite low, except when compared with Mud Lake, and here is seen the third highest index. From this, it might be concluded that, ecologically, Whatcom Rapids is more similar to Mud Lake than to any other habitat shown, and thus, if no other information were available, it could be assumed that a transplant from the Rapids to Mud Lake might stand a fair chance of surviving.

Further inspection of the data shows that Lake Fragrance and Good Pond are ecologically most similar. This is surprising in view of the fact that the two habitats are separated by more than 50 mi. and lie at elevations differing by more than 1,000 ft. Good Pond and Bad Pond, however, lie less than 100 ft. apart, but, according to the SCI, they seem to be relatively quite different. The writer had assumed that the two bodies were connected until subsequent investigation spurred by the low SCI revealed complete separation. Lacking other information, the writer would stake more on a transplant being successful between Lake Fragrance and Good Pond than between Good Pond and Bad Pond —even though the latter two are adjacent. This opinion is supported somewhat by knowledge

TABLE 1

DATA COMPARING VARIOUS FRESH WATER HABITATS IN THE BELLINGHAM, WASHINGTON, AREA USING THE SPECIES COMMONALITY INDEX (SCI)

COMBINATION	TOTAL NO. SPECIES	NO. SPECIES IN COMMON	SCI
Whatcom Rapids Lake Fragrance	28	5	17
Good Pond Bad Pond	24	8	33
Bad Pond Peat Bog	18	9	50
Good Pond Peat Bog	19	6	32
Lake Fragrance Good Pond	22	12	55
Lake Fragrance Bad Pond	24	8	33
Lake Fragrance Peat Bog	23	7	30
Whatcom Rapids Mud Lake	28	11	39
Whatcom Pools Good Pond	23	8	35
Whatcom Pools Bad Pond	21	8	38
Whatcom Pools Peat Bog	21	8	38
Whatcom Rapids Good Pond	26	5	19
Whatcom Rapids Bad Pond	24	4	16
Whatcom Rapids Peat Bog	22	4	18
Fragrance Lake Mud Lake	24	10	42
Mud Lake Good Pond	24	9	37
Mud Lake Bad Pond	25	7	28
Mud Lake Peat Bog	24	7	29
Whatcom Pools Whatcom Rapids	24	9	38
Whatcom Pools Lake Fragrance	28	6	21
Whatcom Pools Mud Lake	27	6	22

common to fishermen in the locality, that trout stocking is much more successful in Good Pond than in Bad Pond—thus the names for the two ponds.

It should be emphasized that the method is useful only if:

1. *Thorough and complete collections are made.* It is obvious that the greater the number of species in common, the greater the similarity of niches, and the more similar the physical attributes to account for the species similarity. Thus, the more thorough the collection, the more valid the results.

2. *The collections are made as concurrently as possible.* This prevents seasonal variation from giving too low an index. If an index is desired which covers a longer period, then of course concurrent collections should be made over several seasons.

3. *Statements such as, "Mud Lake and Bad Pond are twice as dissimilar as are Lake Fragrance and Good Pond," are unwarranted.* It is certainly possible to have a zero SCI but for the habitats to have many similarities.

4. *The method is applied within limited areas where biotic communication between habitats is constantly possible and likely.* For example, it would be unrealistic to compare a pond in New Zealand with one in Washington by this method. Even though the physical attributes of the habitats might be very similar, there is no chance of obtaining a high index.

It is the writer's intention in the future to make more thorough collections of these same areas and of others, and to attempt relating the various indexes to the physical characteristics of the habitats.—*Charles J. Flora, Department of Biology, Western Washington College of Education, Bellingham, Washington.*

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CRAWFORD, DAVID L. 1920*a*. New or interesting Psyllidae of the Pacific Coast (Homop.). Proc. Hawaii. Ent. Soc. 4(1): 12–14.

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ROCK, JOSEPH F. 1916. The sandalwoods of Hawaii; a revison of the Hawaiian species of the genus *Santalum*. J. Aust. Inst. Agric. Sci. 12(3): 1–43, 13 pls.

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Illustrations should accompany manuscript, on separate sheets. Often more valuable than a photograph is a good line drawing, which may be reproduced by the zinc etching process.

Figures and Graphs. Copy for figures and graphs should always be drawn large enough to allow for at least one-third reduction by the engraver. Copy should consist of carefully prepared line drawings in one color only, drawn in India ink on plain white drawing paper or tracing cloth. Co-ordinate paper with lines in light blue (a color which will not show in a photograph) may be used; but co-ordinates which should appear in the finished graph must be drawn in India ink. If original figures may not be conveniently submitted with manuscript, duplicate rough sketches or photographic prints may be furnished to aid the editors in their decisions.

It is strongly urged that an indication of scale be incorporated as a part of all drawings in which magnification and size are critical considerations.

Photographs. Photographs should be chosen for clarity in portraying essential information. They should be printed for contrast, on glossy paper, and should be sent unmounted. They should be identified with serial number written in soft pencil on the back to correspood with list of captions.

Illustrations will be returned to the author.

Tables. Tabular matter should be kept to a minimum. Each table, prepared to conform with *Pacific Science* style, should be typed on a separate page, and its position indicated on the manuscript.

Captions. Readily identifiable captions for figures, graphs, photographs, and other illustrative matter should be supplied on a separate page.

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Proof should be corrected immediately and returned *at once* to Robert Sparks, assistant to the editors. Authors are reminded that the editors will allow only a minimum number of corrections on galley proof. Additions to the printed text and changes in style and content are not permitted.

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REPRINTS

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